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PLANT PHYSIOLOGY

B. M. DUGGAR

L. H. BAILEY
EDITOR

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PLANT PHYSIOLOGY

WITH SPECIAL REFERENCE TO

PLANT PRODUCTION

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A field of sugar cane in southern Louisiana — intensive production. [Photograph from the Louisiana Agl. Exp. Sta.]

PLANT PHYSIOLOGY

WITH SPECIAL REFERENCE TO

PLANT PRODUCTION

BY

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PREFACE

In the preparation of this text and reference book, the writer has attempted to consider both the student and the general reader, interested alike in the fundamental requirements of plants and in plant production. Throughout biological study at the present time increased emphasis is placed on the activities and responses of organisms. It is instruction in this type of biological phenomena that is rapidly becoming a part of the cultural side of education, and the practical value of such knowledge is every day being demonstrated, — notably in agriculture and medicine. Plant physiology finds its practical application in plant production, to which it stands in much the same relation as does industrial chemistry to general manufacturing.

It is somewhat strange, therefore, to find that as a separate course plant physiology is not yet offered in some of the colleges whose purpose is primarily to train persons for practical or rural pursuits. Such students require some fundamental work, and few will become specialists. For this general class of students, and for other readers as well, there seems to be needed a text (1) that shall exhibit a considerable range of material, rather than a few topics exhaustively treated; (2) that shall include both qualitative and quantitative work; and (3) that shall keep in view, as far as possible, the relations of the science to plant production, drawing the illustrations, wherever convenient,

from plants which are familiar and directly useful. By maintaining some direct contact with practical problems, interest is aroused for further desirable fundamental preparation. "The idea that useful knowledge cannot be cultural must be dismissed. . . . Every possible application must be made of each abstract principle." (Eliot, "The Conflict between Individualism and Collectivism in a Democracy," page 66.)

In the field of pure physiology, there are recent texts and guides embodying much of what is considered best in the modern content and attitude of the science. An elaboration of the methods of quantitative study is there indicated, and stress is laid on the materials and energy involved in plant activity. Such books will be consulted with much profit.

In selecting from the great amount of available material that which has seemed to be most suitable for the present purpose, consideration has been given the fact that in many colleges general courses are offered, not only in such distinctively plant lines as agronomy, horticulture, and breeding, but likewise in fields overlapping physiology, or partially included in this subject, such as soils, bacteriology, pathology, and genetics. The subject-matter included is intended to be sufficient for a course of one-half year involving two recitations and two laboratory periods; but it may be made the basis of a shorter course by suitable selection of material, or of a longer course by an extension of the collateral work.

In the preparation of this text I have used freely any available source of information. The subject-matter has been presented at one time or another in class work. I am indebted to Mr. Lewis Knudson, Instructor in Plant Physi-

ology in Cornell University, for many suggestions and for the form of certain sections of the laboratory notes. Some of the illustrations were furnished by others, or borrowed, as credited in the text. Certain of the drawings were prepared by Miss Anna M. Keichline; others by Mrs. B. M. Duggar, of whose constant assistance with manuscript and proof I would express also my appreciation.

B. M. DUGGAR.

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PLANT PHYSIOLOGY

CHAPTER I

INTRODUCTION

THE relation of plant physiology to crop production and vegetation requires no explanation except where physiology and plant production are alike incompletely comprehended. No one may thoroughly understand a modern agricultural problem who has not learned the full significance and scientific relations of the two eminently practical terms "production" and "conservation." The basal field of agriculture is plant production, for upon this animal production is dependent; and throughout all agriculture conservation is necessarily the key to continuous development and success.

Conservation in the broadest sense implies neither waste of the product grown nor waste of the forces and conditions which make high production possible. These forces are the environment under which the crop is grown and the inherent hereditary possibilities within the seed or seed-material.

1. Permanent high production. — Plants form the natural covering of the surface of the earth, and if there is at present no such covering, where the rock is sufficiently

decomposed to be termed soil, it indicates that something is radically wrong with the soil or climate of that region from the standpoint of the permanent occupation of it by man or animal as well as by plants.

Of all object lessons in permanent occupation by plants,

Fig. 1. In the Rainier National Forest, Washington. [Photograph from the Forest Service.]

that of the aged forest stands out supreme. Here a vigorous growth may have endured for centuries, and except for such accidents as those of floods and fires, or of flagrant devastation by man, it might continue for centuries more. So far as may be seen, or measured by the short space of agricultural record, at least, there is with the greater growth of the forest an ever increasing fertility of the land.

From this lesson of production and conservation one turns to another in discouraging contrast, — and that other is this: much of this fertile forest land has been cleared, and year by year fields which were once highly productive are left untilled, or abandoned as of no longer interest agriculturally. If lessened production is the cause of abandonment or discouragement, the system which leads to waste of this nature should have a speedy end.

All of the results of science and practice are needed to assist in working a change in the conditions. Each science may contribute something.

2. The relation of physiology to production. — Plant physiology is an intimate part of scientific plant production. It concerns itself with plant response and plant behavior under all conditions; that is, with all relations and processes readily evident or obscure, simple or complex, which have to do with the maintenance, growth, and reproduction of plants. It is then concerned with vegetation or crops, with the relation of the plant as a whole, and with all special responses or functions of any organ or cell. From the standpoint of physiology one should be able to get facts alike applicable in understanding or interpreting the behavior or yield of plants of all description. The principles of growth are learned by the same methods, whether the plants are those constituting the vegetation of the mill-pond or of the vast fields of cultivated grain; of the greenhouse or of the weedy growth of the neglected lot; of the sparse vegetation of the poor prairie or of the primeval forest. Throughout all, the principles involved are ultimately those of analyzing the complex stimuli and the resulting growth, or maintenance, and reproduction.

Through physiological study it is possible to understand better that which pertains to production, since increased knowledge of plant response makes it more nearly possible to modify opportunely and to improve upon current practices of production, and to develop progressive varieties and strains. Obviously, production involves a variety of nonphysiological conditions, but it also involves physiological conditions, and little progress may be anticipated without an intimate knowledge of the relation of the growth of the plant or crop to the conditions under which it is grown.

3. Physiology and ecology. — At the outset, moreover, it is necessary to recognize two possible lines of study and observation. The one is primarily concerned with the isolated and controlled plant and the functions or responses of its diverse organs and structures. This is generally considered pure physiology. The other line of study deals with plants or the crop in the field, or stated technically, in a natural or seminatural habitat. This is field physiology or ecology. There is, of course, no sharp line between the two subdivisions indicated, and both are important in production. It is necessary to know the plant, and it is equally essential to know the environment, for that is the sum of the conditions to which the plant responds.

4. Physiological processes. — The engineer who does not understand his machine cannot expect to get effective work out of it. He should know its intimate structure, what work it can perform under all conditions, and how it may be controlled. In the same way the plant producer who knows the structure of the plant and its behavior is provided with the means of interpreting the effects of con-

ditions upon the organism. The plant is a delicate physical, chemical, and living mechanism; and through the work which is performed, often expressed in growth, or change of some sort, it is responsive to practically all manner of stimuli.

Under whatever conditions it may be able to grow and reproduce itself there are many phenomena, or processes, which are recognized as fundamentally physiological, although the information respecting these may often be essentially physical or chemical. All modern physiologists are necessarily pursuing physico-chemical methods in interpreting all the activities of plants. Among these processes may be mentioned the absorption, movement, and incorporation of water and of gases; the absorption and disposition of nutrient salts; the manufacture of organic food material; the accumulation, digestion, and assimilation of foods or food materials; respiration; growth and variability; reproduction and heredity; and the special growth or other changes as responses to environmental factors. Much of the material presented in this book is for the purpose of demonstrating simply some of the essential principles involved. Qualitative measurements are frequently sufficient.

5. **Environment.** — The environment of any plant or crop is a complex of factors or conditions as a resultant of which there is the response of the plant in vigorous or weakly production, and in diverse form or habit of growth. Most of the important factors of the environment affecting the agricultural plant are perfectly obvious. In considering these one almost unconsciously thinks of those factors which operate above the soil and those which operate

through the soil. This division of the factors is not wholly satisfactory, as will be seen. Agronomy is commonly subdivided nowadays into "soils" and "crops"; but these do not exclude physiology, they make it, in its broadest relations, more nearly indispensable.

Conditions acting above the soil are mainly sunshine, heat, precipitation, humidity, evaporation, and air movement and composition; while through the soil there is afforded fixity, mineral nutrients, and water, as well as heat and air. There are, however, many other factors acting above or below the soil which may affect vegetation directly or indirectly, including the bacterial flora of the soil, and injurious substances in the soil solution; fungous diseases, insect pests, and higher animals; the constant factor gravity; and many special stimuli.

This complexity of environmental factors renders an interpretation of the effects of any one factor in terms of plant behavior peculiarly difficult. Progress in field study, or experimental ecology, is nevertheless being made, and much is due to the greater perfection in instrumentation as applied to the habitat.

In nature a species of plant thrives best where the requirements of the particular form are most completely met. In the case of the cultivated plant, however, while the natural factors condition production, these alone are, of course, insufficient to determine whether or not a particular crop should be grown in a particular locality, for there are a host of economic considerations which must have weight. Market, transportation, labor, machinery, and many other factors must be taken into account.

From the point of view of the natural factors there are

again two lines of inquiry: (1) Is the crop suited to the general conditions of the region? (2) Are the conditions of environment and the cultural practices afforded the crop such as to result in maximum yield? It is not expected that any considerable number of facts enabling one better to answer the first question shall be presented in this book; such facts, at any rate, may be only incidentally touched upon. The fundamental facts developed should, however, enable one to observe, test, and answer for himself more completely any question which would fall in the second group of inquiry.

6. Crop ecology. — Since ecological data may be included only incidentally, a few words may be said here concerning the general relations of plants as distributed over the surface of the earth or as cultivated under special conditions. In the steppes of northern Africa and portions of Australia, in the dry prairies of the western United States and southern Russia, or in the equivalent regions of western Brazil, the vegetation is similar in physiognomy. Here tough and drought-resistant grasses thrive, and for the most part these regions are treeless tracts where rains fall infrequently or precipitation is poorly distributed, and here, too, winds often exert their highest force. The great permanent grass lands, such as these areas are, may be considered as being ecologically most closely related to true desert.

On the other hand, in tropical or temperate regions of abundant, or at least sufficient, rainfall forests of one type or another find a natural home. It is clear that upon the discovery of North America, the region now included in the United States was, practically speaking, a continuous forest

extending from the Atlantic westward to the region of little precipitation.

Agriculture and commerce have already encroached to an enormous extent upon the natural domain of both the native forest and grazing lands; but in mountainous regions and towards the northern limit of vigorous growth

Fig. 2. Merriam's Life Zones of the United States; Boreal (1), Transition (2), Upper and Middle Austral (3), Lower Austral (4), Gulf strip of Lower Austral (5), and Tropical (6). Dotted parts of the Austral zones indicate humid divisions. [After Cockerell, in Bailey's Cyclo. Agr.]

most small crops become less profitable, and the forest will, through many generations, at least, form the natural boundary line separating agriculture from the Arctic zone. In addition, of course, forests will continue to thrive in the agricultural region where permitted by man.

Furthermore, in taking a bird's-eye view of the forests of the United States there is noticed a more or less striking limitation in range, hence in general adaptability, of many

well-known forest species. Thus the range of white pine as a commercial crop is practically limited to a region extending westward from the New England States to Minnesota, while the long-leaf yellow pine is restricted to the sandy coastal region of the Southern Atlantic and certain Gulf States.

A similar relation of particular crops to one or more factors of the environment is strikingly brought out by those crops especially that are commonly associated with southern climates. Cotton has a relatively long season of growth, and it is restricted in the United States to a region practically below the thirty-seventh parallel, — a region which is, for about seven or eight months of the year, free from frost and with a high mean temperature. Citrus fruits are accustomed to an almost continuous growing season, where frosts are few and severe freezing practically unknown.

A large proportion of the varieties of rice, also restricted to warm regions, may not be grown beyond those sections in which irrigation is possible. Hard wheats gradually lose the quality of "hardness" (high per cent of gluten) when grown in moist regions. The potato is grown from Canada to Texas and from Scotland to Italy. It is interesting to note, however, that in the United States, usually, the yield diminishes toward the South; and, except under special conditions, the crop matures relatively early throughout the United States. Under such conditions average production is but about 85 bushels per acre. With intensive culture 400 bushels is a maximum for some of the most productive lands in the eastern United States, although 1000 bushels have been reported under peculiar

conditions in the far West. In Scotland, with its more or less continued cool climate, affording a long growth and slow maturity of the potato, we find an average of nearly 250 bushels per acre; while a maximum of 1000 to 1200 bushels is commonly attained. At the well-known seed farm of Lord Rosebery a yield at the rate of over 1700 bushels per acre was reported for a particular plot during the past season. Such facts as these cannot fail to be suggestive from the ecological standpoint.

If the more fundamental lines of general physiology seem less a part of plant production or of practical agriculture than the broader relations above referred to, it must be that it is so partly because of the name which has been applied to this subject, and partly to the fact that the methods of instruction necessarily take the student or reader to a far greater degree away from the cultivated field. To a considerable extent this is necessary, for physiology must remain one of the fundamental sciences, and the fundamental attitude should be kept prominent. It has been considered, too often, a subject with merely laboratory applicability. This erroneous view is vanishing as plant producers become more and more interested in the causes which produce results and not merely in the results themselves. Both horticultural and agronomic work have in recent years extended more and more into the realm of pure plant physiology, which should mean that they have extended into that of accurate experimental study, with the plant response as the central feature.

7. The literature of plant physiology. — The literature of this subject is extensive and scattered, as is that of any other science. The student will do well to bear in

mind that while both the brief and the extensive standard works are important, the subject is one which, through its diverse relationships, encourages breadth of preparation and of application; so that frequently physiological texts alone are insufficient. Any standard text is in large part a logical arrangement and correlation of the facts of many separate papers or monographs; and the detailed data respecting any phenomenon should be sought in the special paper.

The rapid strides which have been made in scientific agriculture and horticulture, especially in plant chemistry, soils, and intensified production, have developed a great array of interesting phenomena. This has given a decided impetus to physiological study. Often, unfortunately, the agriculturist has been compelled to go forward without due knowledge of physiology in the interpretation of his results, but this is no excuse for the neglect of the large amount of valuable and sound work which has been done.

Again, it should be further emphasized that many physiological phenomena are only properly understood when they are viewed in the light of physical and chemical theory, and it is frequently necessary that the student who is encouraged to go further shall turn to the sources of information in these fundamental sciences.

8. Physiology and other sciences. — The aim of plant physiology is a definite one, like that of other sciences; it is ultimately to obtain precise information concerning all those factors and forces which are operative within or through the living plant. Facts are derived and laws established in exactly the same manner as in other sciences. It does not stand apart from physics and chemistry, but

utilizes and advances these or any other sciences which may assist in deducing the facts of plant life. Just as chemistry may utilize the plant as an indicator of chemical reaction or chemical fact, so physiology may use or develop chemical facts in analyzing the phenomena of plant life.

In general, a study of physiology must assume or include facts regarding the form and structure of plants; that is, morphology and histology. The more elaborate the morphology of an organism, as a rule, the more specialized and intricate are its reactions. These reactions are those of its constituent units, and the cell is a convenient and necessary unit of structure. The cell is likewise an important physiological unit, and as such requires special consideration.

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CHAPTER II

THE PLANT CELL

CERTAIN aspects of the physiology of complex organisms may be convincingly presented and perhaps adequately understood without necessarily assuming any knowledge of the minute structure of such organisms. In the same way the demonstration of important chemical facts and reactions may be measurably feasible and instructive for those with little or no conception of the significance of atoms and molecules. Nevertheless, in the same way that a knowledge of the atom is indispensable in understanding chemical theory, just so the minute structure and the relations of cells is fundamental in order to gain a comprehensive view of the activities of a multicellular organism.

A century ago it became apparent to a few physiologists that some fundamental physiological problems could find more nearly complete solution only through experimental studies upon the cell. In the time which has since elapsed the relative importance of cell physiology has been more and more appreciated. Advances in this field, however, are necessarily associated with advances in morphology, chemistry, and physics. The development of cell morphology has been dependent largely upon the improvement of the microscope, and of current methods of technique, both of which have now reached a high state of perfection. Physical and chemical theory and method have

undergone profound changes, and the method of these sciences is now the method applicable to a study of all matter. In view, then, of the relationship of cell physiology to morphology, on the one hand, and to physicochemical advances, on the other, a study of the cell has become fundamental for any comprehensive view of general physiology.

9. **The cell a physiological unit.** — Representing the protoplasmic unit, the living cell is ultimately the seat of all those complex chemical and physical changes, or diverse energy transformations, of the living body. As a unicellular organism the cell must act independently in a particular response; in a multicellular body it responds also as a distinct unit, in unison, however, with many other cells associated together as a tissue. In any case it has been by an investigation of the cell that many of the principles of absorption, digestion, assimilation, excretion, and respiration have been demonstrated. The fundamental conceptions of growth and differentiation, of fertilization and reproduction, were only possible through the development of cell study.

Every cell passes through a cycle of changes. Each is a seat of many, if not of all, of the physiological processes characterizing the organism as a whole. In the more complex plants and animals diversity of labor among the cells has developed to such an extent that certain cells are restricted, or specialized, with respect to their activities, but all cells must perform certain fundamental functions necessary to growth, development, and differentiation.

In almost any physiological process, or in the ultimate effects of various stimuli upon the organism, the cell is

"the important substratum of all vital activity." Referring to the cell-theory and the importance of it, Wilson concludes: "No other biological generalization, save only the theory of organic evolution, has brought so many apparently diverse phenomena under a common point of view or has accomplished more for the unification of knowledge. The cell-theory must therefore be placed beside the evolution-theory as one of the foundation stones of modern biology."

10. Early use of the term "cell." — In the earlier studies upon the cell, beginning in the latter part of the seventeenth century, the term was applied to the firm walls alone, from their resemblance to the cells of the honey-comb. When, however, protoplasm, or the living substance within, was later discovered, and its significance as the important morphological and physiological unit determined, the same term was retained for this essential unit of living substance. Nevertheless, with the obvious distinction in mind, the term is still applied to the many cell-forms or cell-cavities, from which all living matter has disappeared, — such cell-forms of many types constituting the great bulk of the conductive tissues of woody plants, and all of the heart-wood, stony tissue, dry bark, and the like.

11. Meristem or embryonic cells. — Structurally or physiologically the term "cell" is now employed to denote the simplest unit into which the organism may be conveniently resolved. It consists essentially of a unit mass of living protoplasm with certain inclusions or surrounding materials.

In plants the protoplasm is usually inclosed by firm often box-like cell-walls. Plant cells are usually so diverse

that it is difficult accurately to speak of a typical cell. Nevertheless, in the higher plants, those cells which make up the meristem, or growing tissues, possess certain characteristics in common, and they may be considered typical in this restricted sense. All other tissues are derived from the meristem, hence its peculiar importance.

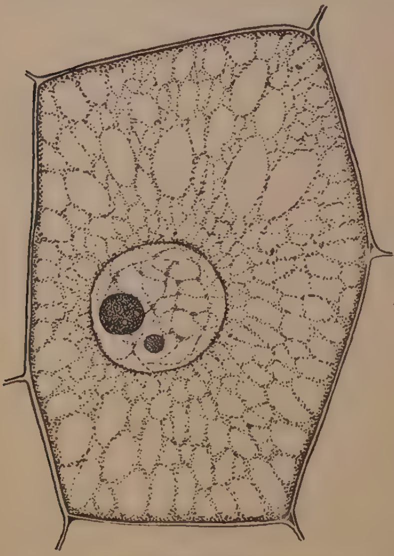

FIG. 3. Cell of the meristem, from root apex of corn.

A vegetative cell of the growing root apex of corn (Fig. 3) is more or less isodiametric in form, often shown as a rectangle or polygon in section. The granular protoplast, or protoplasmic body, differentiated, as denoted later, may be distinguished in such cases with comparative ease. It is closely surrounded by the firm cell-wall which is in general more conspicuous and serves better than the protoplast to differentiate the limits of the cell units. The protoplasm is further differentiated into a dense, often rather centrally disposed, spheroidal body, the nucleus, and a less dense but granular enveloping cytoplasm. In the cytoplasm, when the meristem is included within the green tissues, there may also be noted

certain small refractive protoplasmic bodies termed chromatophores. Vacuoles and food-materials of various sorts may also occur as inclusions within the general protoplast.

An examination of rectangular or polyhedral cells at a short distance back of the tip will reveal certain changes, often denoting a passage from the formative to the non-formative or adult type. In the latter the cell is larger, the cytoplasm less abundant, and much of the cell-cavity may become occupied by vacuoles filled with cell-sap. As the vacuoles form the cell may show radiate or strand-like cytoplasmic areas usually connecting the central with the peripheral cytoplasm, but the nucleus may be still more or less central, and is invariably imbedded in cytoplasm. As the change goes on the sap cavity enlarges and all the protoplasm is drawn to the periphery, the nucleus occupying the center of a marginal mass.

The preceding defines the general type of many of the living cells of the plant body not undergoing rapid growth and division. In the active parenchyma of certain roots, tubers, and other organs to which there has fallen the office of starch or other food-stuff accumulation, the cell may become packed with such products; still, nucleus and a thin layer of protoplasm remain, and these are later essential in the digestion and transport of the stored food-materials.

12. Cytoplasm. — When reference is made to the structure of protoplasm, it is usually the cytoplasm which is considered. Fixing the attention upon the cytoplasm alone, it is found that this feature of meristematic cells, of germinating pollen grains, of the hyphæ of black-mold

fungi, of slime molds, — indeed of all plants, — is much alike. The cytoplasm is evidently a semiliquid translucent substance, and it contains granules, resulting usually in a distinctly granular appearance. All protoplasm is readily killed by a solution of iodine by which it is also stained yellowish brown. This reagent is therefore convenient in demonstrating protoplasm in cells where it is not readily visible. Moreover, the use of a strong salt solution, causing contraction of the cytoplasm from the cell-wall, is also important in demonstration. The outer margin of the cytoplasm, or the margin bordering a vacuole, possesses important physiological characters, and for convenience it is called the plasma membrane. The cytoplasm may inclose food-materials not easily distinguished from the usual protoplasmic granules.

The structure of protoplasm has received much consideration, and three noteworthy conceptions of its form have been advanced as follows: (1) the netted or reticulum theory; (2) the fibrillar theory, and (3) the alveolar or foam theory. The present tendency is to regard it as unnecessary to assign a definite structure persistent under all conditions, and physiologically it is logical to believe that the structure is simply a manifestation of a type of activity. Stains of various sorts have been most important in the study of cytoplasm as well as of nucleus. The chemistry, movement, and special responses of protoplasm in general are considered later.

13. The nucleus. — The nucleus presents the appearance of a dense or refractive protoplasmic mass, and it does contain denser bodies. It is often nearly spherical, but in certain old or specialized cells it may be irregular

in form. It is differentiated from the cytoplasm by a distinct membrane, but the minute structure is only apparent by the use of staining methods. It shows usually a strong affinity for many stains, and its parts may react in a differential manner. In the growing nucleus there is usually a refractive reticulum staining rather lightly in general, but deeply at certain points, or angles, where there is or seems to be an aggregation of chromatic substance. There is also present upon the reticulum at least one nucleolus. This latter is most evident by staining, but in the unstained nucleus it is strongly refractive, and often serves to locate the nucleus.

Nucleus and cytoplasm are interdependent, and few cells are long functional in which either of these parts is killed, or from which either is removed.

14. Plastids. — In addition to cytoplasm and nucleus the other protoplasmic organs of the cell requiring brief mention at this point are dense bodies termed plastids, usually disposed in the parietal protoplasm of the cell. In the higher plants they are usually spheroidal or ellipsoidal in form. Of these there are three types: (1) chloroplasts, containing the pigment chlorophyll, to which is due the green color of plants, essential, as shown later, in the manufacture of organic food-material in the green plant; (2) leucoplasts or amyloplasts, those starch-forming plastids contained in subterranean or other organs of the plant receiving no light, — plastids, nevertheless, which are able, when exposed to light, to develop into chloroplasts; and (3) chromoplasts, plastids of various colors, generally yellowish to red, sometimes crystalline in form, from the presence of albuminous crystals, or from the crys-

tallization of the pigment contained. The special significance of these three types of bodies will require treatment later.

15. The cell-wall. — The plant protoplast is commonly, and in the vegetative organs of higher plants invariably, invested by a firm cell-wall. When constituting a part of a tissue-system, the cell-walls are throughout most of their length in close contact, mutually supporting, and, with the modifications subsequently noted, they form together a complex circumcellular organic skeleton. Some walls are also infiltrated with mineral matters; especially are the outer walls of grasses and the like silicified.

The form of the cell-wall is, of course, in all cases a perfect index of the form of the cell, although in some cases after the death of the protoplasm the cell may be somewhat modified in shape. The wall is formed by the protoplasm and it is properly regarded as a product of protoplasmic metabolism or secretion. It is commonly composed of two or three distinct layers, three often occurring when the wall is strongly thickened. In special cases where successive layers are deposited, the wall may present a laminated structure. In the formation of the cell-wall in general a middle lamella is first laid down. This is the primary layer, and upon it is deposited a secondary, and finally a tertiary, layer. The second layer is, as a rule, the thickest or most completely developed. In the looser tissues of the body the middle lamella may split at the angles between the cells, thus leaving intercellular spaces of greater or less extent, the importance of which in gas diffusion through the plant will subsequently receive special consideration.

The successive layers in the formation of the cell-wall may be interrupted at certain points or along certain lines, and there will thus result pores or pits of various types. Again, the thickening may be confined to particular regions, so that the peculiarities of the wall may be considered due to the deposition of the layers in very limited areas, as in the annular or spiral vessels. In the tracheal tissue these pores may occur in adjacent cells opposite to one another, so that the cells at these points are in reality separated merely by the primary layer. Such connections are important in the transport of water and substances in solution; but it is not the province of the present brief description to make an examination of wall structure, the aim being merely to indicate the mechanism of special physiological interest.

In the case of the soft-rot of cabbage and other vegetables, the causal bacillus attacks and decomposes the middle lamellæ, so that the organization of the tissues is promptly broken down. Gelatinization also of the cell-wall may occur in seed-coats. Flax, mistletoe, and some other plants exhibit this phenomenon when placed under conditions favorable for germination.

16. Cell-sap. — The protoplasm is infiltrated with water, and there are closely associated with it nutrient and other substances in solution. Moreover, as already indicated, there are generally present within the protoplasm some definite "vacuoles," also containing substances in solution; and such solutions are called cell-sap. These vacuoles are apparently of much the same nature as the large central one ultimately formed in the great majority of differentiated cells. The term "cell-sap," at any rate, is

indiscriminately applied to the liquid contents occurring in the vacuolate areas large and small.

The vacuoles are unquestionably of much physiological significance, and certain materials diffuse into such spaces and may to a considerable extent accumulate there. The substances held in solution may include a variety of organic or inorganic compounds, again referred to in the discussion of metabolic products. In some cases the color of plants is due to coloring matters occurring in the cell-sap alone. With respect to the other liquid cell contents the vacuoles may have therefore a certain differential character.

17. Cell-forms. — Young or growing cells in tissues are often somewhat rectangular in outline. When, however, the pressure of adjacent units is released, there is an apparent tendency to assume a form more or less spherical. This should not be confused with the fact that micro-organisms possess a considerable diversity with respect to their specific forms; indeed many unicellular organisms of elongate forms which grow for a time in pairs or groups become also more convex along the lines of attachment upon being set free; thus rod-shaped bacteria may become more rounded at the ends. In the meristem of the growing tip where the cells are closely united, and encompassed by a variety of pressures, the typical form of the cell is isodiametric or polyhedral. Back of the formative region, under the influence of the growth pressures and various other stimuli, there is a tendency for many cells or cell-groups to take up an elongate form. The latter may make possible, in time, other important modifications.

Under all circumstances the embryonic meristem cell

is capable of changing its form or of undergoing differentiation when in a position where this response is called forth. It must be understood that this differentiation is in direct or indirect response to a variety of stimuli which are normally operative during the growth of the plant. It is found, therefore, that while all the cells of higher plants have developed from an original meristem of the type indicated, there is the greatest diversity in the ultimate form, as also in the ultimate work, of the cells differentiated therefrom.

Fig. 4. Cell from a leaf-hair of squash, showing vacuolate cytoplasm, nucleus, and chloroplasts.

The different types are, of course, associated with a specialized form of labor, or function; therefore these cell-types are of peculiar physiological importance, as well as of obvious anatomical and evolutionary interest. The following common types may be briefly characterized for further reference: —

18. Parenchyma. — This type includes various forms

of relatively thin-walled cells which may have undergone very little, though sometimes considerable, change in shape. They are generally more or less rectangular or polygonal in outline, and frequently exhibit large intercellular spaces. In some cases, especially when the protoplasm has been lost, the walls may be infiltrated with mineral matters. In situations where they may be directly or indirectly exposed to the drying action of the air, the walls may contain cutin or suberin, thus rendering them less penetrable to the passage of water. If the walls are thickened at the angles, as in the supporting cells of the cortex, they are commonly termed collenchyma.

Parenchyma of some form almost invariably accompanies conductive tissues, but it is not particularly adapted for the rapid movement of solutions, being in large part dependent upon simple diffusion phenomena. It has been found, however, that in the parenchyma there are commonly minute cytoplasmic connections between adjacent protoplasts; that is to say, minute pores may occur in walls separating cells, and through these pores cytoplasmic fibrils may extend, connecting therefore adjacent protoplasts. These connections may be of great importance in the relations existing between the cells in parenchymatous tissue.

19. Sclerenchyma. — This term is usually employed to denote cells with considerably thickened walls. Thickening may proceed to such extent that the protoplast disappears and the lumen may be practically closed. The grit cells of the fruit of pear are much thickened, and the stone cells of the "pits" of drupaceous fruits, or of the

shells of nuts, are extreme examples. Elongate cells with thickened walls may also be included here, such as bast, or those surrounding the bundles in Indian corn (Fig. 5).

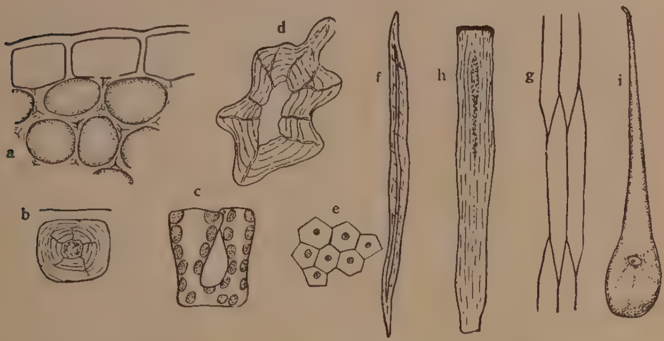

FIG. 5. Some extreme cell-types: collenchyma (*a*); sclerotic cells from pine needle (*b*); and vegetable ivory (*d*); unusual palisade cell (*c*); bast (*e*, *f*); prosenchyma (*g*); from cotton seed-coat (*h*); and stinging cell of nettle hair (*i*).

The term "stereome" has been applied to thick-walled cells serving primarily for support.

20. Tracheids. — These are thick-walled cells, more or less elongate, with walls often showing pitted, reticulate, or spiral thickenings. They may possess a considerable lumen, and the mature cell may show no trace of protoplast. They are usually lignified, and are important in the conduction of water. In many plants (such as the pine and other conifers) they constitute the sole water-conducting system.

These tissues are likewise important in support, and this fact emphasizes a point worthy of special note, and that is

this: a tissue may be primarily important for a specific type of action, but differentiation is not commonly so complete as to render it unserviceable in many correlated activities.

21. Tracheæ or vessels. — The vessels are formed from rows of elongate cells by the absorption of the intervening walls coincident with the disappearance of the protoplasm. Such cell-cavities, or ducts, may extend continuously for several centimeters in length, and they are especially important in the conduction of water in angiosperms generally. These ducts also show usually the annular or spiral thickenings previously referred to. Both this and the preceding type are commonly associated with at least a small amount of parenchyma, and it is probable that their physiological properties depend to some extent upon the latter.

22. Sieve tubes. — The sieve tubes are also elongate cells, but they are peculiar in the fact that the protoplasm in the adjacent members of the cell-row is continuous by means of very distinct connecting pores through the intervening walls. These walls are thickened and form a so-called cell-plate, a perforate plate through which, therefore, the protoplasm is continuous (Fig. 6). Cell-plates may also occur at points of contact in more or less vertical walls.

Another peculiar feature of such sieve cells is the fact that the nuclei become disorganized, but the cytoplasm remains. These cells, however, are in close contact with certain cells which are typical parenchyma elements, the companion cells, the latter containing both cytoplasm and nuclei. The sieve tubes usually occur in the woody

bundles, and are easily identified in the outer part of these (commonly in the bark, therefore, of dicotyledonous plants). They are regarded as most important in the conduction of the less diffusible organic materials.

The arrangement or association of certain of these types of cells and further indications respecting their several functions in the general physiology of the plant are again referred to under growth and transport.

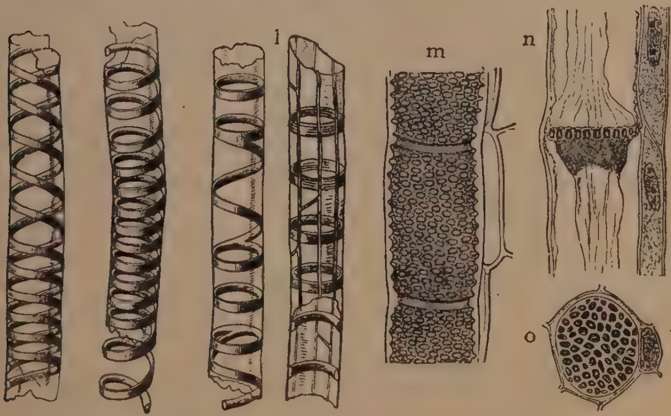

FIG. 6. Conducting cells of fibrovascular bundles, ducts, tracheæ (l); pitted vessel (m); sieve tubes with companion cells, in longitudinal (n) and cross section (o). [Adapted.]

23. Protoplasmic movement. — Naked protoplasmic units or aggregates such as amœbæ, or the plasmodia of Myxomycetes, show a considerable power of locomotion due to streaming movements in the cytoplasm. It is also well established that within the protoplast of a variety of cells invested with a firm cell-wall there is relatively

rapid movement. It is a phenomenon so common[1] that it must be assumed to have physiological significance. Moreover, it is often rapid in cells of large size, so that it seems safe to say that it is not unimportant in facilitating diffusion. A study of this capacity for movement gives an impressive mental picture of the protoplasm as the seat of activity in the cell or member.

The various types of protoplasmic movement are commonly grouped in four categories: (1) simple streaming, (2) circulation, (3) rotation, and (4) orientation.

Streaming movements are rather spasmodic in different parts of the cell, first in one direction, and sooner or later a reversal. Aside from the slime molds, the cœnocytic filaments of the black molds show, among plants, pronounced movements of this type.

Circulation consists in movement at any instant in more than one direction in the cell. The motion may occur in the peripheral cytoplasm, but this type is characteristic of cells possessing cytoplasmic strands. In fact, when the cytoplasmic strands are lost, the movement may become rotary. Circulation may be conveniently observed in the stamen hairs of Tradescantia and in the stem and leaf hairs of various plants, especially cucurbits; also in young root-hairs and other young cells.

Rotation, or the movement in a rather constant current or direction around the cell, or in some area of the cell, is the most striking type. It usually occurs in cells which

[1] For a list of greenhouse material suitable for the study of movement the following paper may be consulted: Bushee, Grace L., The Occurrence and Rate of Protoplasmic Streaming in Greenhouse Plants. *Botan. Gaz.*, **46**: 50–53, 1908.

have lost the cytoplasmic strands. It may be observed in the water weed Elodea, and attains a maximum rate and clearness in an inner parietal cytoplasmic layer of the internodal and other cœnocytic segments of the alga Nitella (stonewort). In this last-named plant it is not uncommon to find, at a temperature of 28 to 30° C., a rate of movement from 3 to 4 mm. per minute.

Movements of orientation result in a gradual, or scarcely directly visible, shifting of a portion of the cytoplasm or of other portions of the protoplast. By this means the nucleus is able to change its position in the cell, and the plastids (chloroplasts) show peculiarities of arrangement under different intensities of light. Orientation is doubtless to a considerable extent characteristic of all living cells, but the result of the movement is more easily noted in those green cells quickly responsive to changes of light.

24. Protoplasmic irritability and response. — The movements previously referred to are indicative of a type of activity. It is of interest to note to what extent this activity may be affected by a change in the environment, as, for instance, a change in temperature. If favorable material of any kind (such as Nitella, Tradescantia, Cucurbita) is carefully studied at different temperatures, effected by a temperature stage, it will be found that with respect to rate of movement there is, in general, a minimum, an optimum, and a maximum temperature for movement, so that the protoplasm is highly responsive to these differences of the environment.

This change in rate of motion with the above-mentioned minimum-optimum-maximum manifestation is obviously an indirect effect. Moreover, since temperature changes

are a constant environmental factor, it is safe to assume that the organism is adjusted to this factor, so that it manifests what is known as a tonic response.

Another case of response has already been noted: under different intensities of light the orientation of the chloroplasts may be diverse. In the cells of the duckweed (favorable for observation) the chloroplasts are distributed in the upper portion, or dome, of the cell and also across the bottom, in diffused light; while in bright light they lie at the sides and one above another. The position in the dark is along the vertical walls, also the horizontal wall when that does not abut upon the epidermis. This type of response to light (in this instance) is generally regarded as denoting protoplasmic irritability.

LABORATORY WORK

Living cells. — Remove with the forceps or scissors the filamentous, purplish hairs from the stamens of any available species of Tradescantia. Mount these, and note carefully the form and size of the distinct cells. Distinguish cell-wall, protoplasm, and colored vacuole, and observe each of these critically. Describe the peripheral and strand cytoplasm, also the form and position of the nucleus, with nucleolus. Draw. Compare the cell drawn with others both nearer the base and the apex of the filament. Kill with tincture of iodine, and examine.

As in the preceding, study the cells of hairs clipped from a petiole of a fairly young squash or pumpkin leaf. In this case note also the form and position of the plastids (chloroplasts). Peel off a little of the epidermis of Cyclamen or Begonia; mount, study, and describe these cells. For comparison study and draw a stained preparation of a root-tip or bud-apex and compare with the previous material.

Cell-forms.[1] — Study parenchyma in the young stem of Indian corn, or in the pith of an herbaceous plant, also collenchyma in the peripheral portion of a stem of wild carrot or squash. Sclerotic cells may be easily identified in the gritty portion of the fruit of pear. Tracheids and tracheæ may be studied by means of longitudinal sections of almost any woody plant, grape vine and squash showing, particularly, ducts of considerable size. These plants are also good for an examination of sieve tubes.

Cells such as the tracheids may be conveniently studied after maceration. Place sections of the desired material in very strong or concentrated chromic acid for about one minute, or until thoroughly limp and easily teased apart; then wash and tease out, or mount immediately, and separate the cells one from another by gentle pressure upon the cover-glass.

Protoplasmic movement. — Following the general indications in the text, study types of protoplasmic movement in the cells of such plants as Nitella and Elodea; hairs of Tradescantia, of a cucurbit, or of Gloxinia; and the young hyphæ of any common black mold, Mucor.

Use the most favorable material for further observation upon the effects of temperature upon movement, employing a temperature stage in determining the rate of movement at temperatures varying from towards the minimum to an approximate maximum. Plot a curve of the results.

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[1] It is considered important that students not qualified in anatomy or histology should devote several laboratory periods to a study of the cell and cell-forms. Reports based upon their own observations may be supplemented by a more complete review of the subject as presented in Stevens, Strasburger, Vines ("Text-book of Botany"), or other suitable text.

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CHAPTER III

THE WATER-CONTENT OF PLANTS AND THE GENERAL RELATIONS OF ROOT SYSTEMS

The life and special activities of the plant or animal are at all times conditioned by the water-supply. Plant growth and production may be more sharply limited within countries, regions, or localities by the water-supply than by any other factor of the ordinary physical environment. A soil which does not receive and deliver to the plant throughout the growing season a reasonably constant supply is a sterile desert whatever may be the quality of this soil with respect to latent mineral possibilities.

Water is often regarded as a crude food-stuff, because it enters abundantly into the composition of living things. It does, in fact, contribute elements to the making of organic food, as shown later; but for the moment it is most important to consider water with respect to its solvent action. All organic food-material presented to the living cell must be in solution; likewise the mineral nutrients and the gases which take part in metabolism. Ordinary plants are constantly in contact with a water-supply, during their growing period, by means of special absorbing surfaces. It is to be expected, therefore, that the forms and functions of plants are to a considerable degree

concerned with the use and distribution of water and of substances in solution.

Properly to consider the use of water there arises the necessity of learning or reviewing the structure of the organs and the nature of the processes whereby water is absorbed, conducted, and eliminated, as well as general

FIG. 7. Thrifty squash-plants as typical examples of the relation of water-content to rigidity.

and special crop relations in which this factor plays an important rôle.

25. Hydrostatic rigidity. — Under conditions favorable for growth, it is obvious that the living cells of a plant are commonly in a state of extension or hydrostatic rigidity. Small and succulent stems are able under such circum-

stances to support a considerable load of branches, leaves, and flowers. Any condition which deprives the plant of water inaugurates, on the contrary, a state of flaccidity; that is, a drooping or wilting. These phenomena will be referred to again, but the fact may not be too strongly emphasized that rigidity and abundant water-supply are closely related, especially where the mechanical supporting tissues do not reach the fullest development. Compare the appearance and vigorous yield of well-watered lettuce, squash, or tomatoes with those unattractive and miserable plants whose leaves or fruits fall limp upon themselves.

26. The water-content of plants. — The growing plant contains invariably a high percentage of water. It is generally stated that an active, succulent plant or tissue, one which contains relatively a small amount of fiber, shows a water-content of 75 per cent or more. When the plant contains a larger number of thick-walled cells, or woody tissues, which may be required for protection, support, or conduction, the percentage of water may be lessened. In every case, it is probable that the active protoplast requires a water-content of from 80 to 90 per cent or more. The necessary water must be obtained by absorption from the environment, and in the case of the common agricultural plants absorption is almost exclusively by means of the root-system.

The amount of water contained in different plants, or, in fact, in the same plant, is subject to considerable variation. Nevertheless, it is instructive to note the composition of a number of crop or useful plants with respect to this factor. The following table will indicate approxi-

mately the average water-content of a number of familiar plants or plant products: —

Plant	Water-content, Weight Per Cent	Plant	Water-content, Weight Per Cent
Apples, fruit	83.2	Cucumbers	96.0
Beets, mangel wurzels	90.9	Oats, cured grain	11.0
Beets, red	88.5	Onions	87.6
Beets, sugar	86.5	Potatoes, Irish	78.9
Beets, tops	87.0	Potatoes, sweet	71.1
Cabbage	90.5	Pumpkin, flesh	93.4
Clover, red, green hay	70.8	Rice, grain	12.6
Clover, white, green hay	78.2	Spruce needles, old, in October	56.7
Corn, dry seed	10.9	Spruce needles, young, in spring	80.6
Corn fodder, green	79.8	Timothy hay, cured	42.2
Corn silage	79.1		
Cowpeas, green hay	83.6		

27. Variation in water-content of different organs. — An examination of the various analyses reported by chemists will indicate that the different products or organs of the same plant may vary materially in the water-content, as would be anticipated. This may be due in part to differences in the amount of supporting or otherwise differentiated tissues. Fruits may, however, contain much more water than the growing shoots upon which they are developed, or certain fruits may contain at maturity very much less. This will all depend upon the nature of the tissues in these parts, and upon the degree of maturity, or the method by which maturity is accomplished.

During the ripening of seeds the water-content may be

reduced by several hundred per cent. This may go on simultaneously with a reduction in the water-content of the plant as a whole, which is the case in cereals and many other plants having a definite growth cycle. On the other hand, the maturity of the seed in many annuals and perennials which grow in an indefinite manner may be wholly independent of any general ripening process of the entire plant.

The seed within the body of the fruit may likewise differ from the latter; thus the seed of watermelon or peach shows, when the fruit is ripe, a water-content far less than that of the pulp which surrounds it. The water of the plant does not merely permeate all parts indiscriminately; it is accumulated within or withheld from organs by virtue of complex histological, chemical, or physical relations. The formation of a few layers of corky tissue may cut off the water-supply of an organ, the storage of solid food-materials may reduce the quantity of water, or the presence of certain compounds may increase or inhibit absorption.

28. The water-absorbing system. — The root-system constitutes the mechanism whereby the water-supply must be secured in practically all higher plants, including the common agricultural plants. There is, moreover, diversity in the form, texture, and distribution of the roots of crop plants. The diversity in form and texture is not necessarily coupled with great differences respecting the water-supply furnished.

There are two general types of root complexes ordinarily recognized. In the one there may be a central or main root called the tap-root, the branches and sub-branches

of which arise in rather irregular order, but make up a general root-system which may occupy a fusoidal, a conical, or an obconical soil volume. This type includes lettuce, parsnip, and a great variety of common plants. In the other type there may be little or no indication of a tap-root, and instead few or many lateral roots of more or less equal size may in a way take its place. Corn, for instance, possesses at the beginning of germination a distinct tap-root, but very soon, under ordinary circumstances, in the soil the length of this may be approached or exceeded by laterals or by whorls of secondary roots originating considerably later (Fig. 8). In many of the small cereals there are produced upon germination several roots which may be termed of the first order, and the direction of growth of these determine for many days the general form of the system.

FIG. 8. General appearance of the root-system of corn at the time of tasseling.

It is a part of the function of the root-system to fix the

plant in the soil, but of chief interest must be regarded the relations of the root-system to the water and the nutrient salts of the substratum.

From a casual examination of plants in the field it is difficult to form a proper conception of the extent of the root-system. Pull up a wheat plant or any fibrous rooted grass, and the root-system may seem extensive. Proceed in the same manner with a beet or with an herbaceous plant like the sunflower. The root-systems which come to view in these two cases would give an entirely erroneous impression of the relative or actual extent of the roots. A large proportion of roots and rootlets remain in the soil, especially in the case of the fleshy plant.

Upon a careful examination it is noted invariably that accompanying vigorous growth in the soil there is a surprisingly extensive system of small rootlets, and these are usually disregarded in rough estimates of root extent. The only methods of determining approximately the root development is either by excavating carefully, and then washing away the soil while the roots are in some way effectively supported, or by growing the plants in special root chambers.

29. The rooting habits of crops. — Plants vary greatly with respect to the distribution of roots in the soil. In the same habitat, or under the same cultural conditions, one plant may show the greater extent of its roots close to the surface, while another may branch more freely at greater depth. Freidenfeld has made a careful study of root-habit in a variety of common plants.

A study of this distribution of roots under diverse conditions is a matter of considerable importance. Upon it

may be based better practices in soil preparation and culture. Investigations upon root distribution have been more extensive at some of the experiment stations in the West, and there are very few data available for conditions in the United States essentially different. Ten Eyck has shown that the roots of the corn, wheat, oats, and other cereals may reach a depth of from three to four and a half feet, the small grains reaching the greater depth. His method consists in supporting the cuboidal mass of soil containing the roots in wire-netting cages, through the meshes of which many steel rods are thrust horizontally. When the soil is washed away, the roots do not break so readily as when unsupported. Nevertheless, this method has many difficulties and involves special apparatus for handling large quantities of earth.

Recently a method has been developed in Russia by Rotmistrov whereby the difficulties experienced in handling large quantities of soil are to a considerable extent eliminated. Some new sources of error have been introduced, but apparently the work has been as well controlled as possible. The method consists in growing plants in the natural top-soil and sub-soil compacted into extensive narrow boxes sunken in the soil during the period of growth. When placed in position, these boxes present a surface 1 inch wide, 20 to 40 inches long, and 20 to 40 inches or more in depth. The roots eventually occupy a volume of earth equivalent in form to that of a narrow slab or broad board. After the desired period of growth it is possible to obtain practically the exact form of the entire root-system by the manipulation suggested. Practically speaking, this consists in the inversion of the root-pene-

trated mass upon a support or screen closely studded with nails. Upon this screen careful washing is subsequently given, and the entire root-system is then readily transferred to cardboard. Figure 9 shows a root-system of the potato grown in this manner. About 30 plants were grown by Rotmistrov in such boxes for varying periods of time.

As a control upon this method some plants were grown in natural soil beds, and the development and extension of the root-systems were studied by means of deep pits with horizontal chinks or tunnels. The pits permitted a careful record of the depth of root extension, and through the small horizontal chinks observation could be made upon lateral penetration.

Working with the pit-and-chink method indicated, it was determined that even in seven days the roots of "a great many cultivated plants extend beyond the limits of the soil when tilled to a medium depth" (8 inches). The roots of winter grain often extend laterally and vertically to a distance of over 40 inches. Winter rye was found to extend to a greater depth, and winter wheat to a greater extent laterally, than other small grains.

Among the roots of corn there may be distinguished, according to Ten Eyck, primary vertical and primary lateral organs. The latter in their course again give off vertical roots. The main laterals grow several feet, and as they reach those of neighboring hills, they also strike downward. Under the rather dry conditions of the West a majority of the lateral roots are within from three to twelve inches of the surface. When the sub-soil is poor, deep culture of corn may therefore kill the roots or prevent their formation in the most fertile parts of the soil. On

the other hand, it is especially necessary under the dry conditions which prevail in that region to have a deep surface mulch. It is of interest to note that under these circumstances shallow cultivation early and deep cultivation later has proved the most satisfactory method.

FIG 9. Root-system of a potato grown to maturity in a deep, narrow box. [After Rotmistrov.]

Kafir corn and sorghum produce roots of the same general type and distribution as those of corn, but the former are tough and fibrous and the laterals are beset with numerous, fine, feeding roots which are to be found between the main laterals and the surface. The upper eighteen inches of soil is very completely filled with these fine roots. Moreover, the plant grows late in the season, and the

mere presence of the numerous tough roots and crowns are sufficient to leave the soil in bad physical condition. This unfavorable condition restricts the absorption of water by the soil during fall and winter, and discourages the requisite preparation for the succeeding crop. Owing to these facts, sorghum land commonly shows a deficiency in moisture the following spring.

The rooting habit of the sugar-beet, according to Ten Eyck, indicates that it is a deep "feeder" at least during the late stages of growth. The roots of potato seem to occupy the soil as completely as any crop, and a considerable number penetrate to a depth of two or three feet; yet many of the deep-rooted individuals possess a surprisingly small number of feeding roots, at least on plants examined in the autumn.

Nobbe measured the root-system of a wheat plant about one year old and found the aggregate length of the roots to be 500–600 meters (545–655 yards), while that of a full-grown pumpkin vine measured about 50 times as long, or about 25 kilometers ($15\frac{5}{8}$ miles). The rooting habits of shade trees are particularly worthy of study, especially in view of the difficulties experienced with trees in towns and cities.

From the studies in narrow boxes made by Rotmistrov it has been shown that a large number of farm crops penetrate both loamy and sandy soils to a depth of one meter or more.

30. The production of root-hairs. — The roots and minute rootlets which in a complete root-system are readily evident to the eye are, however, secondary with respect to the relations existing between the plant and the soil

water, or the soil solution. When the plant is removed from the soil, even most carefully, organs smaller than the rootlets are not made evident. There are, nevertheless, numerous minute, simple, and effective structures generally present in abundance. These are the root-hairs arising from the surfaces of all young and growing roots.

Fig. 10. Radish seedling, showing root-hairs.

If seeds of radish or squash are placed in damp moss or germinated between sheets of moist filter paper, or in any of the germinators subsequently described, the root-hairs become evident (Fig. 10). As soon as the root has attained a length of an inch or more there are developed at a short distance behind the tips a large number of these structures. They arise practically perpendicular to the surface, and a microscopic examination indicates that they are simple, siphonaceous cells consisting of a rather resistant cell-wall within which is contained the granular protoplasm and cell-sap.

When grown in the manner indicated, the root-hairs may be perfectly straight tubes. As they develop in the soil, however, where the numerous sharp soil particles obstruct their growth, they bend about and flatten out against and around these particles, becoming, as a result, contorted or deformed in appearance. It is evident that

they come into the most intimate contact with the minute soil particles, — so intimate, at times, that fine particles actually stick into the walls (Fig. 11). They are, therefore, peculiarly fitted for the needs of absorption, as will be later developed.

It will also be noted that those regions of the rootlet clothed with root-hairs have ceased to elongate; that is, so soon as the hairs are developed it is an indication that this portion of the root is fixed in the soil; otherwise its growth would crush such organs and prevent their further efficiency. In this connection it may, therefore, be observed that the "push" which is needed to force the root forward in the soil is concerned with a relatively short axis, perhaps not more than a quarter of an inch in length. The practical advantages of this mode of growth are obvious upon a moment's reflection. If, for instance, one should attempt to force into the soil a fine wire two feet long, pushing from the upper end, it would certainly bend. In fact, the difficulties of such a mode of growth in the soil practically precludes the possibility of its occurrence.

FIG. 11. Root-hairs (*a*) grown in coarse sand; cortex (*b*) and epidermis (*c*).

The root-hairs are relatively short-lived upon the majority of plants. Their activity may be embraced in a period of from a few days to a month or two, and they are readily injured by

unfavorable conditions of the environment. The ability of a plant to take water from the soil, moreover, will depend in large measure upon the extent of these simple organs. It has been estimated that the surface of the system in corn is increased from five to six times by favorable root-hair production; in barley about twelve times, and in Scindapsus about eighteen times.

Fig. 12. Root-tip of corn, diagrammatic.

31. Root-hairs and the water-content of the soil. — It is only in exceptional cases that land plants develop few or no root-hairs. In general, where few are present, the plant will wilt with a higher water-content of the soil than when more are provided. Root-hairs are considerably suppressed in the case of corn, wheat, and other crop plants when the soil is saturated. Nevertheless, many plants continue to produce such organs in water cultures, even though the number of these organs or the individual length of each may be greatly reduced. In the soil so long as the plant does not wilt, it appears to be generally stimulated to most abundant root-hair production at a moisture content somewhat less than that which will afford the highest yield.

It is commonly assumed that darkness is an immediate factor in the development of the root-hairs, but this assumption does not appear to be sustained by experiment. Relatively strong, diffused light with adequate water-

supply does not inhibit root-hair production in the ordinary crop plant; but with strong light it is more difficult to maintain a high moisture content under laboratory conditions.

32. The root-cap. — A longitudinal section of the tip

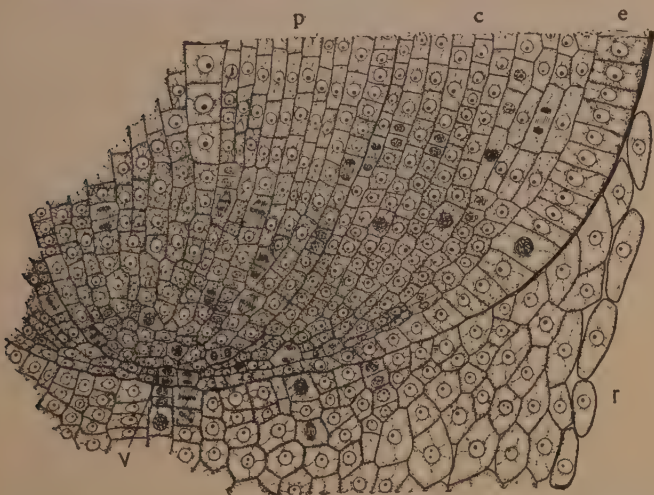

FIG. 13. Root-tip of corn, high-power study of formative region: epidermis (*e*), cortex or periblem (*c*), plerome (*p*), and root-cap (*r*). [After Curtis.]

of the root (Fig. 12) shows a rather complex but interesting structure. Protecting the growing tip, there is invariably found the well-known structure called the root-cap. The root-cap consists of a mass of cells to which falls the duty or office of a bumper organ. It is very effectively developed by divisions in the epidermal (protodermal) cells of the growing tip parallel to the surface. This mass

of cells is always resistant and compactly arranged within; but as the cells are pushed outward, becoming old and sloughed-off by the continual addition of new cells, they undergo gelatinization and decay. This latter process, however, is important, for the gelatinization of these cells doubtless acts as a constant lubricant to make easier the course of the tip progressing through the soil.

33. Structure of the root-tip. — In the root-tip proper there is a primordial meristem (Fig. 13) or region of rapid cell division. It is often called the formative region, and it is from this portion that the differentiation of tissues proceeds. In some cases the meristem is relatively extensive, as in the pea and certain other legumes, while in the example given (corn), barley, sunflower, and others, it is limited to very few cells, — differentiated tissues extending practically to the morphological apex.

The central portion of the root-tip is occupied by the plerome or central cylinder, a columnar mass of cells, most of which elongate considerably at a short distance back of the tip. In longitudinal section they appear as a rectangular type of cell in all that portion of the root unoccupied by root-hairs, but many of these cells are later transformed into the primary woody bundles. The central cylinder is surrounded by a cortical portion termed the periblem, made up at first of rather isodiametric parenchymatous cells. The inner layer of this periblem is commonly differentiated by thicker walls to form a more or less definite sheath or endodermis. The external layer of the root-tip is the epidermis, also composed, in the immediate tip portion, of cells generally isodiametric. It is from these epidermal cells that tubular outgrowths

develop as root-hairs. It is believed that factors operating to increase rapidly the longitudinal extension of these cells will decrease the number and length of the root-hairs.

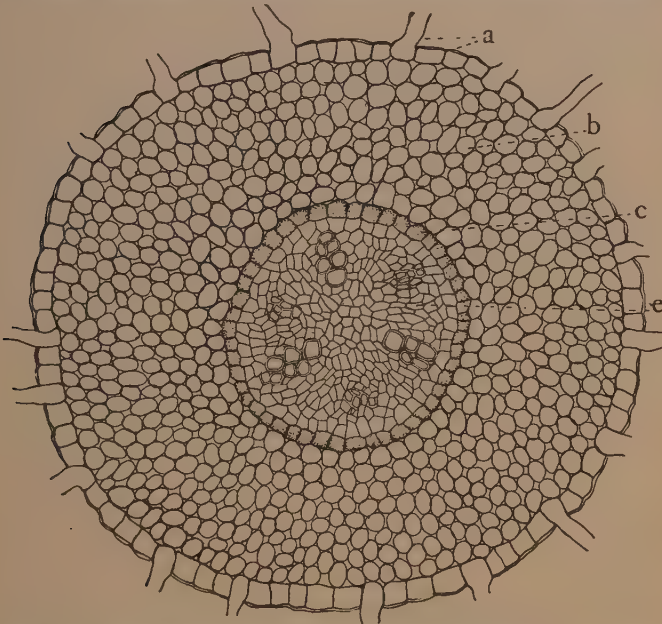

FIG. 14. Cross-section of a rootlet: epidermis and bases of root-hairs (*a*), cortex (*b*), endodermis (*c*), and central cylinder (*e*) with xylem and phloem elements.

It would seem that in some cases the retardation of growth by soil particles has a beneficial effect upon hair production. In a completely saturated air or in a high temperature — in other words when the conditions are such as to rapidly promote increase in length of the cortical cells of

the root — there is a tendency to suppress hair production.

34. Soil particles. — The extent of the root-system previously discussed enables the plant to come into contact with an enormous quantity of soil particles. Each particle of the soil, even air-dried soil, is invested with a film of water, and the amount of water which the soil may contain is, to a considerable extent, dependent upon the degree of fineness of these particles. It is also dependent upon the amount of organic matter, the so-called humus, as subsequently indicated.

Fig. 15. Seedling from a sand culture, showing adherence of grains.

With respect to the sizes of the particles, a soil may be designated as sand, silt, or clay. These three classes are subdivided into types or grades, depending upon the minuter differences in size of the particles. The following table is generally adopted by soil experts for the purpose of a mechanical classification: —

Coarse sand	$\frac{1}{25}$ - $\frac{1}{50}$ inch diam.
Medium sand	$\frac{1}{50}$–$\frac{1}{100}$ inch diam.
Fine sand	$\frac{1}{100}$–$\frac{1}{250}$ inch diam.
Very fine sand	$\frac{1}{250}$–$\frac{1}{500}$ inch diam.
Silt	$\frac{1}{500}$–$\frac{1}{2000}$ inch diam.
Fine silt	$\frac{1}{2000}$–$\frac{1}{5000}$ inch diam.
Clay	$\frac{1}{5000}$–$\frac{1}{25000}$ inch diam.

All soils contain, in addition to larger particles, certain

proportions of these general constituents. In addition a fertile soil must contain a considerable amount of humus derived from the disintegration of plant and animal remains.

35. Soil texture and water-holding capacity. — The water-holding capacity and the capacity for delivering water to the plant will depend, therefore, to a very considerable extent upon the mechanical constitution. In general, a fertile soil should consist of relatively fine particles, since the water-holding capacity and the amount of food-materials will be, up to a certain point, a factor of the fineness of the particles. On the other hand, fineness of particles at or approaching the point of saturation of the soil may cause exclusion of air to such an extent that the finer the soil the less the amount of air present. In this connection, however, it should be remembered that under ordinary circumstances the pore space of a clay soil may be 50 per cent of its volume, while that of a coarse sand uniform in texture may not exceed 30 per cent.

One cubic foot of an ordinary loam would cover a relatively enormous area if spread out as a single layer of particles. It is calculated that the contents of one cubic foot would cover about one acre. Some sort of mental picture of the absorbing system and its possibilities may be had by recalling, in conjunction with these indications respecting soil particles, the extent of the root-system as clothed with root-hairs. The root-system of a mature sunflower may almost completely permeate a cubic yard of soil.

It is necessary to make a comparison of some main soil

types with respect to the water-holding capacity in order properly to understand the relation of the plant to the soil. The water-holding capacity of the soil as ordinarily measured is the ratio of the weight of water, when the soil is at the point of saturation, to water-free soil, or dry weight of soil.

The following table is an indication of what may be expected in this regard in certain general soil types: —

Ordinary sand	20– 30 per cent
Rich sandy loam	30– 40 per cent
Rich clay loam	40– 60 per cent
Very heavy clay	60– 70 per cent
Garden soil, rich in humus	70– 90 per cent
Humus	100–300 per cent

It is considered to be a general rule that a large number of cultivated plants find most favorable conditions for rapid growth when the soil contains from 40 to 50 per cent of its maximum water capacity. In the case of a sand, therefore, with a maximum capacity of 25 per cent the optimum for plant growth would be 10 to 12½ per cent. This will depend somewhat, however, upon the other conditions under which grown.

Under the conditions encountered in the laboratory and greenhouse, where in general the soil employed has been well stirred, or is constantly well aërated, the optimum moisture content may be much higher. In some cases this optimum may run as high as 70 to 75 per cent. Under field conditions it is apparent that the amount of organic matter and the aëration of the soil are most important in determining the optimum. When organic matter is abundant in the soil, especially when the soil is compact, a

tendency toward saturation apparently encourages a type of bacterial action which may promptly result in great harm to many agricultural plants.

36. Exceptional plants. — The preceding statements relative to the optimum water-supply are to be understood as applying to a great majority of cultivated plants; however, as an example of an exceptional crop the cranberry may be cited. This plant grows to the greatest advantage in typical bog situations. As ordinarily cultivated, drainage is given this crop in such manner that the surface soil will not contain free water; yet under ordinary circumstances the soil approaches saturation on account of the low water-table, — at the same time bog conditions are such as to retard oxidation. The cranberry and many other bog plants are therefore adjusted to the peculiar conditions of their habitat. These bog conditions are, in fact, extremely interesting, but it is unnecessary to go into this subject further at this point.

37. Unavailable water. — The plant is unable to withdraw all of the film moisture in contact with the soil particles. If at any time the plant is unable to obtain from the soil the water it requires, wilting will ensue. The water then remaining in the soil is unavailable or non-physiological. When this point is reached, the soil is dry to the touch, yet an appreciable percentage of water remains. For any plant the film water unavailable in a variety of soils is proportional to the water-holding capacity of these soils; that is, the greater the water-holding capacity the greater the pull against the plant when the content is low.

Under ordinary agricultural conditions with loamy soils, there will be from 5 to 12 per cent of water unavail-

able for most cultivated plants. This may be reduced to less than 1 per cent in coarse sand, and may rise to more than 50 per cent in typical New York muck. The tables which follow are after Heinrich[1]; the first shows the relation existing between water capacity, hygroscopic water, and unavailable water; the latter table gives a suggestion as to the conduct of different crops on two types of soils: —

Soil	Water-content at Saturation	Hygroscopic Water-content	Water unavailable to Plants
	Per cent	Per cent	Per cent
Coarse sand	26.5	0.42	1.5
Medium fertile garden soil	43.9	1.68	4.6
Infertile sandy muck	41.4	.97	6.2
Sandy loam	43.3	2.40	7.8
Very fertile calcareous soil	38.3	3.65	9.8
Peat soil	274.0	20.60	49.7

Plant	Moisture Content at which Plants begin to Wilt	
	On Calcareous Soil	On Peaty Soil
	Per cent	Per cent
Oats	8.4	32.3
Barley	9.98	33.3
Rye	9.55	32.8
Red clover	10.28	34.3
Potatoes	5.07	41.4

[1] Cited by Cameron and Gallagher, Bureau of Soils, U. S. Dept. Agl. Bul., **50**: pp. 57–58.

It will be noticed that so soon as the amount of water in ordinary soils becomes about three times the hygroscopic content it begins to assume physiological importance. A soil which contains merely hygroscopic moisture is "air-dry"; and if this amount only, or any amount less than "available," were present, the soil would actually withdraw water from the plant, thus inducing drying-out independent of transpiration.

The following table, compiled from Hedgecock, includes certain agricultural plants as well as species inhabiting marshy and xerophytic conditions: —

PLANTS GROWN IN LOAM, UNDER SIMILAR GREENHOUSE CONDITIONS

PLANT	UNAVAILABLE WATER
Coleus (*Coleus blumei Benth.*)	3.0
Morning glory (*Ipomœa purpurea Roth.*)	4.1
Cabbage (*Brassica oleracea L.*)	5.8
Corn (*Zea mays L.*)	5.9
Sugar-beet (*Beta vulgaris L.*)	5.9
Wild rye (*Elymus canadensis L.*)	5.9
Oats (*Avena sativa L.*)	6.2
Asparagus (*Asparagus officinalis L.*)	7.0
Lettuce (*Lactuca sativa L.*)	8.5
Cucumber (*Cucumis sativus L.*)	10.8
Arrowhead (*Sagittaria latifolia* Wild)	15.6
Pondweed (*Potamogeton americanus* C. and S.)	24.8

It will be noted that plants normally inhabiting water or swamp-land wilt first, and next to these are cucumber and lettuce, both with high-water requirement and relatively little structural protection against water-loss.

38. Leaves poorly fitted for water absorption. — In general leaves are of little practical value in the absorption of water. On a hot day a wilted plant recovers after a shower, not because it absorbs water rapidly through the leaf parts, but because (1) the atmospheric conditions then generally reduce the amount of transpiration, and (2) the roots are able promptly to get the water needed. Nevertheless, partially wilted lettuce or peach leaves will be revived if the blades are dipped into water, even though the cut ends of the petioles are exposed to the air. A flax plant or a cabbage leaf would show no perceptible effect from the immersion for a long time.

On the other hand some plants are capacitated for the absorption of water through leaves or pitcher-like vegetative organs. Among these are certain of the Bromeliaceæ (a family to which the pineapple belongs) possessing leaves the bases of which sheathe the stem so closely as to form reservoirs for precipitation water. In this family, moreover, the absorption of water is more abundant by means of certain cells in the peculiar shield-shaped scales, and *Tillandsia usneoides*, the Florida moss, is an extreme form in this respect. It is an epiphyte, consisting of thread-like stems and narrow leaves, very common on trees in the far South. This plant is provided with much the same type of water-absorbing hairs which give the entire surface a glistening appearance. The aërial roots of orchids and some other tropical plants are provided with velamen, a chambered epidermal tissue which may absorb water like a sponge.

LABORATORY WORK

Water-content. — Determine separately the water-content of any convenient twigs and fruits, or of fruits and seeds; — apples and apple twigs, squash and squash seed are generally available. If crude scales only are accessible, use from 50 to 100 grams of material; while if very delicate scales are employed, 10 grams are sufficient. The process may be as follows:

FIG. 16. A dry-heat sterilizer, serviceable also in determining water-content.

(1) weigh and record weight of vessels to be employed, preferably small glass, aluminium, or tin dishes; (2) mince or break up the material finely, using a quantity more or less than that which is desired, into the proper vessel, weigh immediately, and record; (3) dry at from 100 to 110° C. to *constant weight* (if a constant temperature dry-oven is at hand, leave in this until the

next period; otherwise dry in any oven used for dry sterilization during two successive laboratory periods), weigh, and record. If not weighed immediately, leave the material in a desiccator over fresh (dry) $CaCl_2$ until determined. Calculate percentage of water.

Determine the water-holding capacity of any rich garden loam, sand, and powdered quartz which may be available for later experiments. To completely saturate the material a simple method is to fill a small pot or wire basket with the moist material, tamp down lightly, dip into (or pour on) water carefully until slightly more than saturated; then, as soon as the drip has ceased, dump approximately the quantity desired into the weighed vessel, and proceed as before. In calculating the water-content of soils it is to be remembered that at present the method more commonly employed is to determine the ratio or percentage of water, with respect to dry weight of soil, a calculation easily made as follows: $r = \frac{w - w'}{w' - w''}$, in which w = weight of saturated soil and vessel; w', of dry soil and vessel; w'', of vessel; r being the per cent of water.

Root-systems. — The distribution of roots in the soil may be studied by careful excavation and washing out (cf. Ten Eyck, Kansas Agl. Exp. Sta. Bul. 127). A far better conception of the fine root-system (under fairly natural conditions only when care is taken in the manipulation) may be obtained for demonstration, according to the method of Rotmistrov, by growing plants in flat zinc, or zinc-lined, boxes which for class purposes are large enough if 1 inch across, about 15 to 18 inches wide, and 18 inches deep. The box should contain surface-soil and sub-soil well compacted and arranged as in some local soil type. During the period of growth the boxes should be immersed to the surface in deep boxes of sand or soil. Growth should be permitted to proceed for a month or more. When the boxes are open, a side is removed, a fine mesh wire screen (about ¼ inch) is laid on the soil, the whole being inverted; the soil is left upon the screen, and upon dipping this gradually into water an almost perfect root-system may be obtained.

Root-hairs. — Germinate seeds of radish and barley in a germinator[1] (or upon sawdust or moss) and in moist soil.

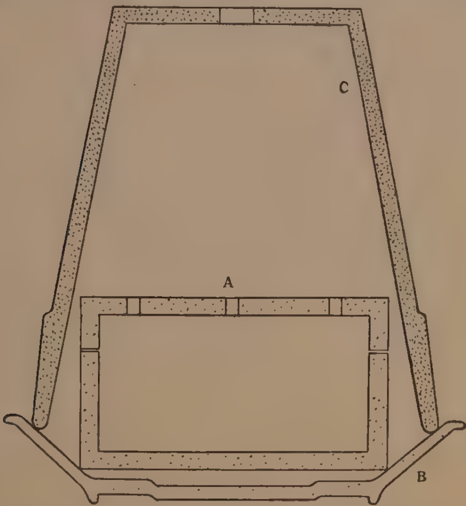

FIG. 17. Germinator for dry room: aërated chamber (*A*); saucer (*B*); and flower-pot (*C*).

Compare under the microscope the length and appearance of the root-hairs, — the plants from soil being carefully washed and small rootlets mounted for observation.

[1] Germinators of a variety of types are employed in various physiological or seed-testing laboratories. In general, any device which secures constant moisture for the germinating seed is satisfactory, but in no case should any materials be employed which encourage the growth of molds or bacteria. Commonly it is sufficient to distribute the seed so that they shall not be in close contact one with another upon the surface of moist sphagnum moss, sawdust, or other moisture-holding materials of this nature into which the roots will readily penetrate.

The type of vessel employed is of little consequence so long as there is

Root-cap. — Make a preparation of the whole root-tip of barley and note with the low-power of the microscope the general extent of the root-cap, the histology of which may only be studied by adequate sections.

Root-tip. — Make longitudinal sections of the root-tip of corn or sunflower and compare with those of pea or vetch, distinguishing and describing primordial meristem, central cylinder, plerome, epidermis, and root-cap. Hand sections are sufficient, if properly made, but prepared slides are also desirable.

Unavailable water. — Use young plants of cucumber, lettuce, and barley or wheat grown under similar conditions in small pots of rich or heavy loam and pure sand or quartz [preferably those soils the water-content of which were determined earlier]. The pots should contain no moss or such material at the bottom. When wanted for the experiment, the plants should be barely supplied with adequate water, so that during the laboratory period incipient wilting may begin. At the moment of wilting of each plant weigh out a portion of the soil of the pot and record the weight. These samples are retained and subsequently dried to determine the content of unavailable water in the different types.

Water absorbed by leaves. — Secure leaves of lettuce, peach,

good aëration. Seed grown for physiological purposes should not be turned over or shaken during germination, as curvature of the roots is likely to result. In testing seeds for vitality, where numerous varieties or sorts are employed, special boxes with ruled spaces, each space designed for a given number of seed, are important. Information regarding this matter may be obtained from any bulletin on seed-testing.

In the laboratory it is often desirable to obtain root-hairs in full development; in such cases flower-pots or special porous germinators (covered saucers) may be employed. With small seed, such as lettuce, mustard, etc., the procedure may be as follows: moisten the germinator or pot and sling a few seed against the inner surfaces. They will adhere to the surface at convenient distances apart, and then if provided with sufficient moisture, absorbed through the walls of the vessel, a rapid and vigorous germination will result, and the development of root-hairs will be shown in a simple and striking manner.

bean, cabbage, cudweed, or other plants available. Some of these should be leaves readily wetted, and others provided with a bloom, or with hairs effectively preventing wetting. Permit the leaves to wilt slightly, then weigh each kind accurately upon a delicate balance. Next place the leaves in water in a dark chamber, immersing all parts except the petioles (or, previous to weighing, seal the petioles carefully with wax). After from 6 to 24 hours note any change in the rigidity in the leaves; also remove all moisture from the surface with filter paper, weigh carefully, as before, and compare the weights of each kind.

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Texts. *Goodale*, *Jost*, *Pfeffer*, *Sachs*, *Sorauer*, *Stevens*.

CHAPTER IV

CONDITIONS AND PRINCIPLES OF ABSORPTION

The physical and chemical factors governing the absorption of water and of solutions have long been the object of careful study. Many phases of such work have been developed in connection with plant physiology. The main facts, however, belong, in large part, to physics and physical chemistry; yet an appreciation of the essential principles is necessary to an adequate understanding of the mechanism and work of absorbing organs.

39. Imbibition phenomena. — Organic bodies of the most varied nature are able to take up water. Commonly, where this water is held within the body by capillarity or surface tension, and where there is produced also more or less swelling, the combined phenomenon is recognized as imbibition in a physiological sense. The hardest wood may absorb water by imbibition, and the force exerted in swelling or warping is capable of lifting or sustaining heavy weights; — sometimes made use of in splitting solid rock or stone. Dry seed-coats generally exhibit a high degree of imbibition, although these may be infiltrated with substances preventing the absorption of water, and in that way germination may be delayed.

In the living plant imbibition phenomena are of im-

portance, and particularly important in the activities of the nonliving cell-walls. The maintenance of the water-current or water-content of the plant is conditioned by imbibition, but under the conditions of growth the inflow of water into the cells of the root surfaces is effected by the force of osmosis, a mental picture of which is essential to an understanding of absorption phenomena.

40. Osmosis and diffusion. — Osmosis and diffusion as generally understood determine the inflow of water to the root-hair, as well as that of the nutrients or other substances (solutes) in solution. These forces are likewise important in the interrelations existing between cells.

The fact of diffusion is readily observed. If a crystal of copper sulfate is placed in a tumbler of water, the salt goes into solution, and in time the colored solution diffuses itself equally throughout the water. This diffusion is wholly independent of any convection currents due to changes of temperature, and it is true for all such soluble substances as sugar, common salt, and the like.

The movement of the particles of the dissolved substances from the region of greater concentration to that of less implies a force, or pressure, which may be termed osmosis, or diffusion tension.

41. The demonstration of osmotic pressure. — The osmotic action of a solute, in water as a solvent, may be conveniently demonstrated qualitatively by a simple experiment in which it is made evident as hydrostatic pressure. A factor not yet mentioned which is involved and which is absolutely essential in this demonstration is a semipermeable membrane, an imbibition membrane which, in this case, permits water to pass through readily,

but is impermeable, or very slowly permeable, to the substance in solution. Semipermeable membranes are of the most diverse sorts. A piece of pig's bladder, a commercial article readily obtainable, is a very satisfactory membrane. This, after being soaked in water, is tied tightly over the bell end of a thistle-tube (Fig. 18) with waxed thread. The solution to be tested, preferably a known strength of some solute, say 20 per cent sugar, is carefully poured into the stem of the thistle-tube (easily accomplished with a guide-wire, or without when the tube is clean and wet) until the bell is filled with the sirup. The tube is then lowered into a vessel of water until both liquids, which should have come to room temperature, are at the same level, when the tube is clamped to a support. It is well to add about 1 per cent of formalin to both liquids as a preservative.

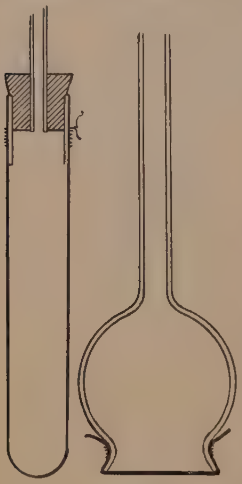

Fig. 18. Diffusion shell and thistle-tube for demonstration osmoscopes.

If the experimental conditions are properly carried out, the liquid in the thistle-tube will rise perceptibly in a few hours, and an experiment to be continued a day or more will require at the outset an extension of tubing. There is, therefore, a major flow of water through the membrane to the strong solution; thus there is manifest a pressure which, if it could be completely measured by this column of water in the apparatus, would be the osmotic pressure

of the 20 per cent sugar solution. If there were a less concentrated sugar solution in the outer vessel, or any solution of salts containing fewer solvent particles per volume, the major flow of water would still be inward, and the extent of this pressure would be in direct proportion to the difference in number of solvent particles.

Special diffusion shells (Fig. 18) are also prepared for demonstration experiments, and these likewise give quick results. In this connection it might be mentioned that accurate measurement of osmotic pressures involves special apparatus in which the natural membrane is replaced by an artificial precipitation membrane deposited in the interstices of a porous cup, the pressure being indicated by a mercuric manometer. The original of this apparatus, described by Pfeffer in 1877, has been greatly improved in recent years by Morse.

42. An explanation of osmotic pressure. — In the thistle-tube demonstration experiment it was suggested that the molecules of sugar or other solute tend to diffuse, to distribute themselves equally, but the semipermeable membrane retards and almost prevents this outward diffusion. The inflow of water is conceived to be in direct response to this force, analogous to a pressure, and the water would continue to flow inward until equilibrium between the pressures were established. This commonly accepted view of osmosis regards the solute as obeying the laws of gases. At a constant temperature, therefore, the osmotic pressure varies with the density or concentration; that is, with the number of particles of the solute. The molecular weight of cane-sugar (a nonelectrolyte) in grams, 342, dissolved in water to 1000 cc. (called a gram-

molecular solution, or M solution), would give, according to this, an osmotic pressure of 22.4 atmospheres.[1] Ordinarily the osmotic pressure of an epidermal cell of a leaf or of a meristem cell is somewhat more than 4 atmospheres, or about .20 gram-molecular (7 per cent) of sugar as determined by the method subsequently discussed.

The plant cell behaves very much as the simple osmometer above described. The root-hair, for example, is a case in which the cell-sap is the strong solution, the limiting layer or edge of cytoplasm is the plasmatic membrane (the cell-wall in this instance furnishing support and protection), and the soil water is the weak solution. The flow of water is into the cell; in fact, under such circum-

[1] A gram-molecular solution of such substances as potassium nitrate or common salt (electrolytes) yields a pressure higher than 22.4 atmospheres. This is explainable on the ground that the number of particles in solution is increased by the partial or complete dissociation of the molecules of such substances into their ions. Thus KNO_3, when partially dissociated, yields in addition to KNO_3 the ions K^+ and NO_3^-. Gram-molecular solutions of this salt show a pressure of about 35 atmospheres. For this reason cane-sugar and potassium nitrate are not osmotically equal; that is, isosmotic at the same molecular strength. Before the theory of dissociation was developed De Vries determined that organic substances such as sugar have about two thirds the osmotic value of monovalent salts; that is to say, that the ratio of their coefficients is as 2 to 3. This ratio and those developed by De Vries for dibasic or other compounds are fairly satisfactory as indications of the isosmotic relations at the strengths corresponding to the plasmolysis of higher plants. Nevertheless, since the per cent of dissociation varies considerably among the salts of the monobasic, dibasic, or other groups, it is essential in any comparative quantitative work to know accurately the per cent of dissociation of any electrolyte employed. This may be obtained from physical chemical tables. The discussion of the relation between electrolytes and nonelectrolytes and the formula for comparing the latter with the former is developed in the work by Livingston, cited in the literature.

stances, so long as an equilibrium has not been established, and water is available, there is absorption of water, and there is manifest always, with adequate water-supply within the cell, an hydrostatic pressure known as turgor. This turgor, existing throughout the plant, is, as already indicated, the chief cause of the rigidity of leaves and succulent shoots. Turgor is then the expression of the osmotic pressure of the cell. This turgor may be measured by simple experiments conducted as described below.

43. Plasmolysis and wilting. — If the root-hair or any equivalent cell is placed in a solution stronger than the cell-sap, the major current of water will be outward, so that water will be withdrawn from the protoplasm, the latter contracting from the cell-wall. This state of contraction is termed plasmolysis. Plasmolysis throughout a

FIG. 19. Lettuce plants in solutions: *A*, tap water; *B*, 2.9 per cent sodium chlorid.

tissue or organ results in flaccidity or wilting. In Figure 19 are shown two lettuce plants transferred from soil. The roots of plant *A* were put into water, and those of *B* into 2.9 per cent sodium chlorid (approximately .5 gram-molecular). The latter has caused a prompt loss of water by the plant, so that wilting has resulted.

If slices of beet or potato are placed in solutions similar to those just mentioned, turgescence on the one hand and

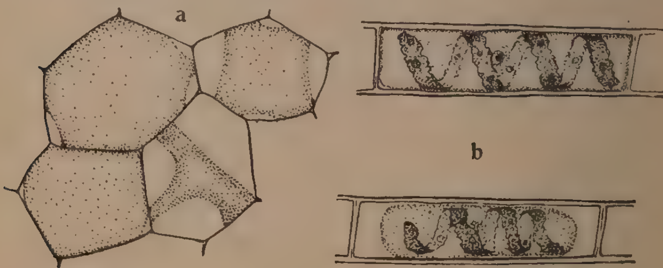

FIG. 20. Successive stages in plasmolysis: epidermis of Tradescantia (*a*) and cells of Spirogyra (*b*).

flaccidity on the other will result in the same manner. The phenomenon of plasmolysis in the cell is sufficiently important to be carefully studied. It is often more readily observed in a cell with colored contents, or numerous chloroplasts, so that the cells of filamentous algæ, the colored epidermis of certain begonias, or of *Tradescantia zebrina,* also the stamen hairs of Tradescantia and Anagallis, are convenient materials for demonstration. Figure 20 shows successive stages in the plasmolysis of the epidermal cell of *Tradescantia zebrina* and of Spirogyra. The concentration which will just cause the least trace of

plasmolysis is taken as the measure of the turgor of the cell.

Plasmolysis may be regarded as a general phenomenon, yet it should be observed that the cytoplasm may undergo contraction, wholly independent of osmotic relations, under the influence of certain stimuli. Greeley[1] ascertained that low temperature may produce this effect, and under certain circumstances high temperature may also cause contraction. It has long been known that injurious substances may produce plasmolysis coincident with injury, a fact to which also Osterhout[2] has recently called attention.

44. Variation in turgor. — Considering plants as a whole, thus including fungi, algæ, and the higher plants, there is great variability in turgor. The fungi show the greatest range and are therefore adapted to thrive in the most diverse situations with respect to concentration. Fresh-water algæ and all the higher plants show, on the whole, a less extensive range; yet even in the same plant the cells of different parts, or tissues, may show no significant variation. Commonly, as already suggested, the turgor in many epidermal and parenchyma cells is equivalent to about 7 per cent of sugar (4.5 atmospheres, but often the range may be from 4 to 8 atmospheres). This fairly close range in the higher plants is perhaps to be anticipated, since it is not conceivable that the strength of the soil solution, under the complex physical and chemical conditions, would show unusual extremes. It may be readily shown by experiment, however, that in a strong

[1] Greeley, A. W., *Am. Journ. Physiol.*, **6**: 112–128, 1901.

[2] Osterhout, W. J. V., On Plasmolysis. *Bot. Gaz.*, **46**: 53–55, 1908.

solution plants develop a somewhat higher turgor than when grown in an extremely weak solution.

According to the work of De Vries many plant cells are just plasmolyzed at a concentration of about 1.2 to 1.4 per cent KNO_3 (.12 to .14 gram-molecular solution), which is equivalent to about 5 atmospheres. Active cells of the cambium may require a concentration of from .4 to .5 gram-molecular solution; and in an investigation of medullary ray cells in a common willow (*Salix fragilis*) Kny finds that the different types of these cells are plasmolyzed at concentrations varying from .10 to .8 M. Moreover, turgor varies with age, nutrition, and with environmental factors, such as heat and light.

In general, observations upon living cells render it perfectly obvious that turgor is usually an essential attribute of active cells. There is, unquestionably, an important interrelation between turgor and growth; therefore, conditions affecting turgescence affect simultaneously all growth processes.

45. Substances active in producing turgor. — No one compound or group of compounds is responsible for turgor. It may be due to dissolved substances both organic and inorganic, and while, in some cases, it does not change materially during the growth or other activities of the cell, yet the composition of the sap may undergo a relatively great change. According to Pfeffer, the turgescence of cells in the root of the sugar-beet is produced largely by cane-sugar, while in the sunflower more than 40 per cent may be represented by potassium nitrate. The beet contains relatively little sugar when young, and the sunflower little nitrate. Various other inorganic salts, glu-

cose, organic acids, and many other compounds are also important in the osmotic strength of cells. The high turgor of certain mold-fungi growing upon concentrated solutions has been determined to be due to organic substances, which may be readily produced within the cell.

46. Osmosis and the absorption of nutrient salts. — The water requirement is not the only one with which osmosis is concerned, for the principles of osmosis and diffusion govern also the absorption of nutrient salts; likewise, of course, the absorption of any other substances present in the soil solution. Moreover, the plasmatic membrane is to a degree permeable to all the nutrients, and to many other substances as well.

Each substance in the soil solution has its specific tendency to diffuse, and it therefore tends to come to equilibrium with the tension of the same substance in the cell. The cells which are active in absorption have in turn a relation to those adjacent to them, and this relation, emphasized or otherwise modified by cells especially capacitated for conduction, extends to all parts of the complex organism. The root-hair, then, in so far as it is permeable, absorbs each substance or solute particle independently, and in accordance with a certain attraction for, or use of, that substance in some way, as in the deposition in an insoluble form — it may be in the building up of protoplasm, or in the accumulation of complex food-materials.

One of the most remarkable facts respecting the osmotic relation of the plant to the soil solution is that there is so little exosmosis, or outward diffusion of substances from the plant, — substances present in the plant but not in the soil. Again, it is difficult to understand the absorp-

tion, transport, and final accumulation (often without change) of certain substances in special organs. There are a number of factors affecting such relations, but much is yet unexplainable on a physical basis.

47. Protoplasmic permeability. — It is an obvious fact that the plasma membrane is permeable to certain solutes, else no growth could result. It is as clearly apparent that this membrane is impenetrable to certain other solutes, and this implies selective absorption. The fact of impermeability becomes evident from a simple observation upon colored cell-sap, and especially so upon contemplation of the phenomenon of plasmolysis in cells containing colored sap. The colored cell-sap of a red beet or of a cell from a stamen-hair of Tradescantia does not diffuse into the surrounding water so long as the cell is uninjured. Moreover, when such cells are plasmolyzed, there is, with continued health, no noticeable exosmosis of the colored material. From dead cells there is prompt diffusion of the colored sap. In this connection it is also to be remembered that in many cases red or blue color in plant cells is merely an indication of acid or basic substances, and this color may be changed in the living cell if it is permeable respectively to basic or acid compounds.

Pfeffer has clearly demonstrated important facts regarding permeability through his experiments upon the penetration of dye stuffs. Methylene blue at a strength of 1 part to 100,000 of water yields a solution which is not visibly blue unless observed in a layer several centimeters thick. It would not therefore give an evident coloration in a plant cell. It is found, however, that upon being placed in such a solution certain root-hairs, Spirogyra,

and other cells are quickly colored blue. It is evident that there has been penetration, and further that there has been accumulation of the dye. In some cases this accumulation is particularly noticeable, due to the formation of a granular precipitate, as in Spirogyra. These facts give some faint idea of the complexity of the problems of cell absorption.

In accordance with the foregoing statements it is possible to assume that when a mixed solution is presented to a root-hair, certain substances, independent of their concentration in the environment, may be absorbed, while others, whether dilute or concentrated, will fail to enter. Upon this ground the relatively abundant occurrence of iodine in seaweeds may be explained. In seawater iodine is present at very great dilution, about .000001; yet it is accumulated in marine algæ to such an extent that it has yielded (and still yields upon the coasts of Japan) a commercial source of this material. Similar and striking examples may be found from a study of the ash content of any plant; thus the content of potash, iron, phosphoric acid, etc., may be greater than the ratio of these substances in the soil solution, whereas other substances may be absorbed in relatively less quantity. The ash content of plants, however, is discussed at greater length later.

It is scarcely practicable to consider here some of the factors which have been found to affect permeability and selective absorption. It is necessary to observe, however, that Overton has developed an interesting theory of absorption based upon certain facts. One of these facts is that substances may be assembled into diverse groups

with respect to permeability, and there has seemed to be some relation between the capacity to penetrate and the solubility of the solute in cholesterin or other similar compound. This has naturally led to the assumption that some such substance constitutes an important part of the plasma membrane. Nevertheless, there are many exceptional cases, and different plants frequently exhibit marked specific peculiarities.

The differences in penetration referred to are characteristic also of toxic or injurious compounds as well as of nutrient or beneficial substances. This fact is frequently of service in explaining the relative toxicity of different reagents. Nowhere is this shown more clearly than in the experiments of Brown, from which it is evident that the seeds of barley may be placed for a considerable time in a relatively strong solution of sulfuric acid without injury, whereas mercuric bichloride rapidly effects an entrance and kills the cells. Further details of this experiment are cited later (section 263). The illuminating experiments of Kahlenberg on osmosis demonstrate clearly that the nature of the semipermeable membrane is a matter of great importance in osmotic phenomena. Furthermore, it has been shown that external conditions, including those of temperature, light, and nutrition, affect permeability and selective absorption to a high degree. The plasma membrane should be regarded as made up in part of a variable and complex colloidal solution.

48. The rôle of diffusion and osmotic pressure. — From what has been brought forward respecting osmosis and diffusion it can be said that these forces are conspicuous in the work of the cell. The concentration of the cell-

sap above that of the soil solution, or other liquid environment, conditions a turgor, an expression of osmotic force. This turgor is coexistent with growth. It likewise confers upon cells or organs a substantial rigidity. The concentration of osmotically active substances manifest through the absorbing surfaces represents a constant pull upon the environment for water, so that root-hairs are able to abstract water from surfaces or solutions which do not represent a greater pull. The plasmatic membrane is extremely complex with regard to permeability, and it may exhibit marked powers of selective absorption. In simple (few-celled) plants osmosis and diffusion may be all-sufficient in what is practically the movement of solutions, but in higher plants there are, in addition to these important forces, also other factors affecting mass movement along the special conducting paths of the fibrovascular system, as noted later.

49. Sap or root pressure. — The absorptive capacity of the root, conditioned by its osmotic relations, may give rise to a pressure, termed root pressure or sap pressure, which may be manifest within the plant whenever the greater rapidity of transpiration does not create a negative tension.

Bleeding phenomena are evidences of this pressure. During the spring, in particular, the maple, birch, grape, potato, black nightshade, nettle, and a variety of other woody and herbaceous plants bleed profusely. In some cases bleeding is checked by drying-out, by the deposition of solid or glutinous matter, and by growth processes (tyloses) filling up the vessels from adjacent cells. In other instances corky layers may be formed sooner or later.

The amount of the exudation may vary from a few drops to several liters per day. Large quantities have been reported for a few plants, especially tropical or subtropical forms; thus Humboldt reports for the American aloe 7.5 liters per day, or about 1000 liters during the entire period; while if the observations of Semler are taken, *Caryota urens* may produce 50 liters per day, the maximum amount observed. Among agricultural plants employed in demonstration work, the potato and tomato are good for short observations, and the grape vine — less subject to decay — for more extended experiments. Eckerson finds that among common greenhouse species, *Fuchsia speciosa* and *Begonia coccinea* are especially favorable for quantity. The pressure under which the exudation is produced necessarily bears no relation to quantity of exudate. The following table, taken from the data of Eckerson, indicates what may be expected of satisfactory material in experimental studies: —

Plant	Mean Quantity in cc.	Duration of Flow, Days	Mean Pressure in Atmospheres
Begonia coccinea (Begonia)	168	29	.858
Chrysanthemum frutescens (Marguerite)	40	9-21	1.014
Fuchsia speciosa (Fuchsia)	99	12–34	1.246
Helianthus annuus (Sunflower) . . .	30	16	1.276
Lycopersicum esculentum (Dwarf Stone tomato)	13	5	1.164
Pelargonium zonale (Horseshoe geranium)	15.5	10	.881

A demonstration of the quantity of liquid produced, and of the existence of root pressure, may be made by comparatively simple methods. The quantity is readily determined by cutting off the plant an inch or two above the surface of the ground and connecting the stump by rubber and glass tubing with a measuring glass protected against evaporation. For the proper demonstration of pressure a suitable manometer is required (Fig. 21).

LABORATORY WORK

Imbibition; swelling of wood. — Use small blocks of oak, basswood, and pine, practically cuboidal in form, preferably cut so that tangential, radial, and longitudinal axes are represented. Mark opposite points of each axis with a pencil and measure carefully with the calipers provided. Then soak the blocks in distilled water for from five to ten days, changing water each day; after which, remeasure each axis and compute the percentage of change.

Heat of imbibition. — Reduce 100 grams of common starch to a uniform powder, dry in an oven at about 105° C., and at the same time, for a control experiment, dry 100 grams of quartz flour or graphite. Cool both powders to room temperature in a desiccator, and pour each into a Dewar flask or

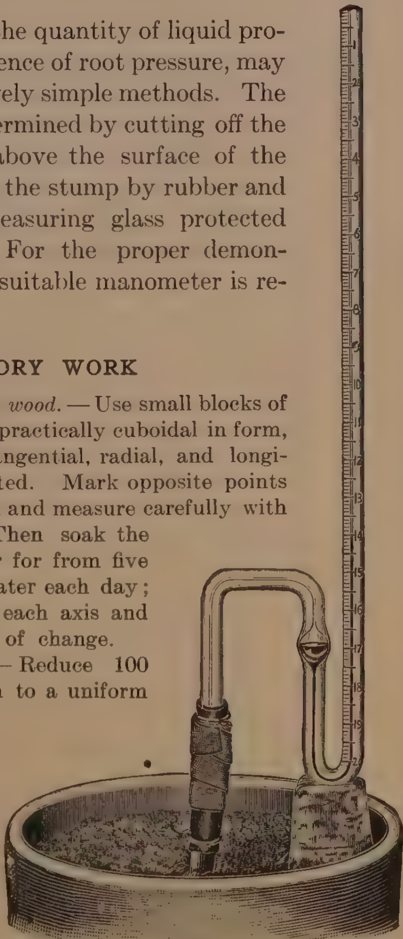

FIG. 21. Ganong's manometer. [After the Bausch and Lomb Optical Company.]

small thermal bottle (a tumbler may be used when double-walled vessels are unavailable). Take the temperature of each powder, then add 100 cc. of water at the same temperature, stir promptly with a clean wooden stirring rod (the starch mixes with water less readily), observe the temperatures, compare, and discuss the results.

Osmoscope. — Set up an osmoscope as indicated in section 41, using a thistle-tube and membrane, or a diffusion shell. Different strengths of sugar solution, 20, 40, and 60 grams per 100 cc. of water, may be used to note differences in rate of flow and total height of column, but no accurate quantitative results are to be expected. Describe the results obtained.

Precipitation membrane. — Drop a crystal of copper sulfate into a bottle containing 5 per cent potassium ferrocyanide, and observe the formation of a semipermeable precipitation membrane of copper ferrocyanide, and the prompt rise of an irregular column of solution inclosed by this, which grows and may attain considerable proportions in fifteen minutes. More neatly, the precipitation membrane may be studied by employing a more dilute solution of potassium ferrocyanide (2 per cent) in a dropper bottle into which is lowered cautiously to its position a dropper tube with capillary outlet, containing a single drop of strong copper sulfate. Note and describe the phenomena taking place.

Plasmolysis and wilting. — Prepare 250 cc. of .5 gram-molecular (M.) solutions of potassium nitrate and of sodium chlorid as stock solutions. From these solutions make dilutions in small vials, capacity about 25 cc., to contain the following strengths of each of the above solutions, namely, .10, .20, .30, and .40 molecular (M.); also one vial with distilled water as a control. In each of the dilutions place a seedling of some plant (root as nearly entire as possible) with delicate stems, or leaf stalks, such as lettuce, radish, or mustard. Observe the dilutions in which wilting occurs, and note the time required in the solutions in which it occurs. Compare the equivalent strengths of the two salts. The above experiment will illustrate the withdrawal of water by strong solutions and will suggest

the progressive plasmolysis and wilting of the cells of the plant through the root-system, but the osmotic strength of the cell-sap may be more accurately studied through the next two experiments.

Osmotic pressure of cell-sap; observation upon tissues. — From the stock solutions used in the preceding experiment prepare in stender dishes or Syracuse watch glasses dilutions which shall contain the following strengths, .10, .12, .15,. 18, and .20 molecular (M.). Split the apical portions of several flower stalks of the dandelion (or other scape which has been found suitable) each into four approximately equal parts. These strips will curve outward, the epidermis being within or on the concave side. Dip strips momentarily into water in which spirals will be formed, then cut into distinct rings. Place one or two of the rings in each of the above solutions and also in distilled water. Follow and note the changes which occur. Further curling of the strips indicates absorption of water, that is, the solution is too weak; no change in the curvature indicates a solution equal in osmotic strength to the cell-sap (isosmotic with the cell-sap); and elongation or reverse curvature indicates loss of water and plasmolysis. Intermediate dilutions may also be made, and the threshold of plasmolysis more accurately determined.

Osmotic pressure of cell-sap; direct observation upon plasmolysis. — The osmotic pressure of the cell-sap may be determined fairly accurately by direct observation upon the plasmolysis of the cell, employing as the plasmolytic agents substances which penetrate the cell only very slowly. The substances employed above, also other neutral salts, cane-sugar, etc., may be used. Cells with protoplasts the limits of which may be easily seen are best for preliminary study, especially algæ, such as Spirogyra, Pithyophora, etc. All precautions as to the cleanliness of vessels, also purity of the reagents and distilled water, should be observed.

From the stock solutions of the monovalent salts previously used prepare for a preliminary test a small quantity of a .2 M. solution. Mount in a drop of this solution one or two filaments

of the alga, observing under the microscope for ten minutes whether there is or is not some plasmolysis. Then, according to the result, prepare dilutions of less or greater concentration, and determine accurately the threshold of plasmolysis. For accurate work the hanging-drop culture may be employed. Determine the osmotic strength also in terms of cane-sugar. Peel off some of the lower epidermis (with colored cell-sap) of Cyclamen or *Tradescantia zebrina*, or use leaf hairs of a cucurbit, and determine the osmotic strength of these cells.

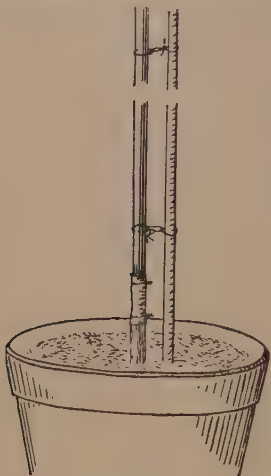

FIG. 22. Simple method of demonstrating exudation from a decapitated plant.

With cells of any plant just distinctly plasmolyzed determine if turgor may be restored by irrigation with tap or distilled water.

Shrinkage. — With any of the above plant material mounted in water measure accurately with the ocular micrometer a cell easily located. Draw off the water and add successively stronger salt solutions until approaching the point of plasmolysis; remeasure; plasmolyze the cell, and again measure. Compare the results with respect to shrinkage.

Protoplasmic permeability. — Into a solution of methylene blue, 1 part to 100,000 parts of water, place a seedling of radish or mustard with well-developed root-hairs; also filaments of Spirogyra and a sprig of Elodea. In two hours examine the root-hairs, the cells of Spirogyra, and the leaf cells of the Elodea for penetration of the dye, and discuss the results.

Sap or root pressure. — Utilizing suitable plants in the open, or potted specimens, determine the amount of water exuded upon decapitation, and also the pressure of exudation in two

species of plants (see section 49). In determining the amount of exudation, conduct in each case the liquid into a graduated test-tube with foot, in which test-tube is placed a drop or two of oil to prevent evaporation. In the pressure determination employ a Ganong manometer, or one similar in principle improvised from materials at hand. Observe frequently, calculate the pressures at the different intervals, and draw curve of results.

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Texts. *Barnes, Ganong, Jost, Pfeffer.*

CHAPTER V

TRANSPIRATION AND WATER MOVEMENT

The water-content of a plant is no index of the amount which has been absorbed throughout its life by the root-system. It is a thoroughly familiar fact that water is commonly eliminated from the plant as water-vapor. This elimination, termed transpiration, is important and should receive special consideration. A very large proportion of the water absorbed by plants is transpired; that is, it passes into the atmosphere by diffusion through the leaves and other delicate parts. This loss of water may be very simply demonstrated by placing a potted plant under a bell glass, taking the precaution to place a rubber cloth over the pot and over all possible evaporating surfaces except the plant itself. In a short time a mistiness upon the glass will indicate roughly the loss of water.

50. Observations upon transpiration. — The demonstration of water-loss may be made in a variety of ways, best of all by loss of weight. Nevertheless, single leaves and abscised branches or organs may be employed in various potometers, by means of which there is measured the water absorbed, this latter corresponding in the end, of course, very closely to that which is given off. Interesting experiments may be readily set up with single leaves or shoots (Fig. 23). By another type of experiment

individuals growing in the field[1] may be made the objects of observation and comparative study.

Experiments made with abscised branches may not be typical, for the shoots are in abnormal relations, lacking the usual organs of absorption, as well as the special soil conditions; and since there is, further, a certain response to the injury received, the results of experiments made with plant parts do not, perhaps, represent the loss under natural conditions. These parts may be employed, nevertheless, for demonstration and for determining more or less accurately the relative rate of loss under different conditions.

Transpiration may be most accurately determined by using potted plants, observing the precautions indicated with respect to evaporating surfaces, and weighing at successive intervals. Special recording balances have been constructed and used for this purpose, but ordinarily such devices are unnecessary to demonstrate principles and limiting conditions.

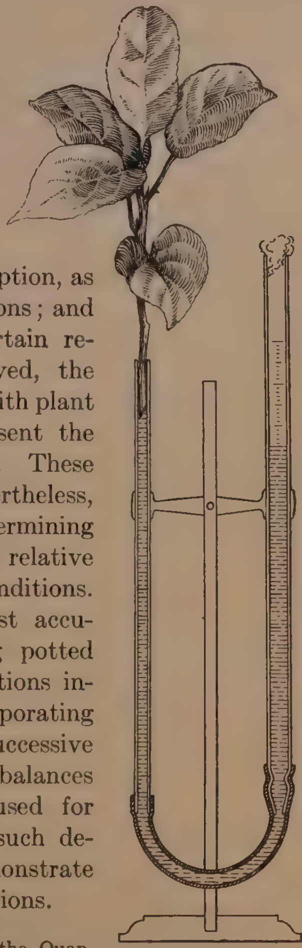


Fig. 23. Burette potometer; shoot fitted with rubber tissue.

[1] Freeman, G. F., A Method for the Quantitative Determination of Transpiration in Plants. *Bot. Gaz.*, **46**: 118–129, 1908.

On a large scale, a rapid loss of water from plants is familiar to all in the process of hay-making. The difference in weight between green and dry hay is perfectly obvious. There may, of course, be a slight loss of water from the cut surfaces of the stems, but even should these be sealed by paraffin or wax, wilting and loss of water will proceed almost as rapidly as before. Practically all parts

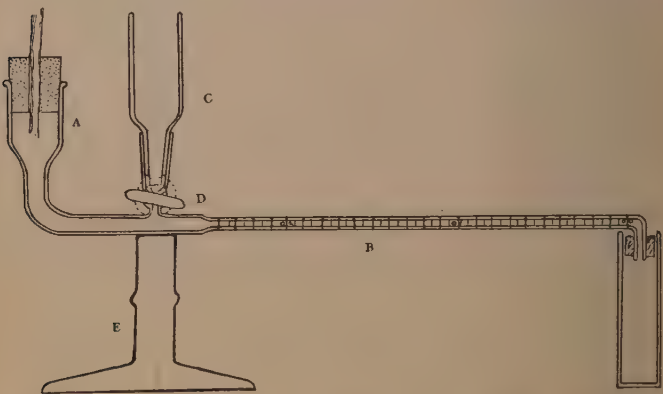


FIG. 24. Potometer with shoot-chamber (*A*), small-bore record-tube (*B*), water-reservoir (*C*), and stop-cock for refilling tube (*D*), supported by base (*E*). [Adapted from Ganong.]

of plants lose water to at least a slight extent. Apples or potatoes stored in a fairly dry situation during a considerable period of time will show considerable loss, although the normal surfaces of such parts are so constructed that rapid drying-out is prevented.

As soon as wilting takes place, sufficient practically to close the stomata, the rate of loss will drop, and thus

the effect of closure of the stomata is made evident in the otherwise more or less normal curve of evaporation.

51. Amount of transpiration. — According to Haberlandt, a corn plant may transpire during a single growing season 14 kg. of water, a hemp plant 27, and a sunflower 66.[1] That is to say, a sunflower may transpire more than

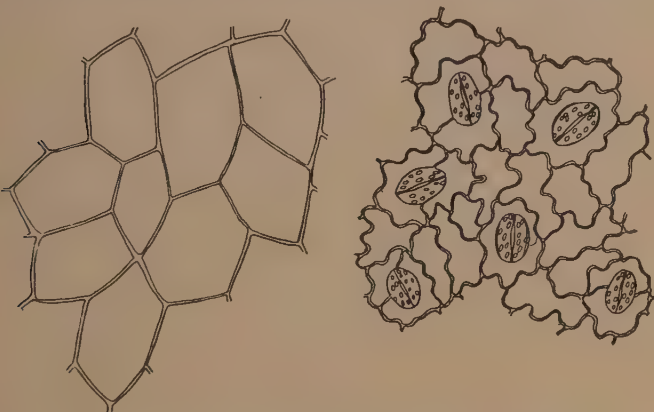


FIG. 25. Portions of epidermis stripped from a leaf of Cyclamen: upper epidermis to the left (no stomata), lower epidermis to the right (6 stomata).

500 grams per day throughout its entire season, which would mean a very much greater amount during a day of maximum loss. Estimated from the transpiration of a small plant, an apple tree of, say, 30 years old might lose 250 pounds per day, possibly 36,000 pounds during a growing season. Therefore, one acre of 40 trees would represent a

[1] The indications are that these figures are far too low for conditions in the United States generally.

water elimination of about 600 tons. Land covered by grass or clover may lose during the growing season from 500 to 750 tons of water, almost entirely through the surfaces of the growing plant.

52. The mechanism permitting transpiration. — The elimination of water from the surfaces of plants takes place because of the fact that the leaves or other surfaces are not wholly impermeable to water-vapor. In the case of delicate, especially young, leaves or shoots there may be some loss of water directly through the epidermis, which is then relatively uncutinized, or otherwise unprotected against water-loss. In many instances this amount is

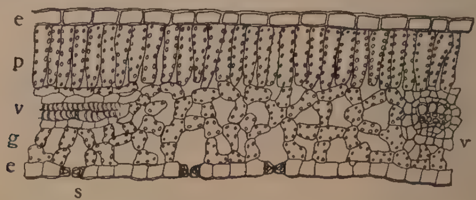


FIG. 26. Section of tomato leaf: epidermis (*e*), palisade tissue (*p*), parenchyma (*g*), vascular bundles (*v*), and stomata (*s*).

negligible, and just as the continuous cuticle commonly absorbs practically no water, so it does not permit of elimination. The epidermis, however, of one or of both surfaces of the leaf and of other delicate parts may be provided with numerous pores or stomata (Figs. 25 and 26) which are the most important means of communication between the internal tissues and the external air.

The stomata open and close in response to complex internal conditions, and under certain circumstances external factors may perhaps play at least a secondary

rôle, as later developed. They usually open into a substomatal cavity which, in turn, is in communication with the intercellular spaces, or aëriferous system. Since the leaves are the organs commonly active in transpiration, it is necessary to note the structure in a typical case.

In Figure 26 there is shown a cross-section of the leaf of tomato. There is a single epidermal layer (e) on each surface, a single palisade layer (p), and the mesophyll or leaf parenchyma. Small veins, or fibrovascular bundles, in cross and longitudinal section are also shown. In the lower epidermis there are several stomata. Many leaves show a multiple palisade, and there is considerable diversity generally in the form and compactness of the tissues.

Each cell of the leaf is directly or indirectly in contact with the air spaces, and ultimately with the substomatal cavities, so that the mechanism is a physical system permitting diffusion. The protoplasm of each cell is thoroughly penetrated with water; it is in contact with the penetrable cell-wall, an imbibition membrane, which is therefore moist. From such moist membranes water-vapor passes into the intercellular spaces, which have a tendency to become saturated. Under external conditions favorable for evaporation there is a high gradient with respect to the external air, so that water-vapor diffuses rapidly from the substomatal cavity through the stomata.

As a result of the work of Brown and Escombe it is clear that the stomatal system in such a plant as the sunflower, for example, constitutes an extremely efficient multiperforate septum, the form and distance apart of the stomata commonly permitting, when they are open, a diffusion almost as rapid as though there were open space. This

is a fact of peculiar interest. Furthermore, it has been calculated that the capacity of the stomata in the sunflower, for example, is about six times as great as any observed transpiration; that is, the stomata only one sixth open would be sufficient to accommodate the most rapid loss of water which has been observed.

The stomata exhibit a considerable range in size, but according to Eckerson the average approximates $18 \times 6\ \mu$. This minute size is scarcely appreciated until one compares it with some visible perforation, such as a needle-prick made with the smallest sewing needle, which is relatively enormous, measuring about $600\ \mu$ in diameter. Nevertheless, the total maximal stomatal opening of an average leaf is approximately one nineteenth of the surface.

53. Distribution of stomata. — While stomata may occur in the epidermis of any plant organs, they are commonly confined to the aërial surfaces, and especially to the leaves, or to organs performing the functions of leaves. As a general rule, in fact, it may be said that the under surfaces of the leaves are the situations most important with respect to stomatal occurrence. Eckerson has found that only about two fifths of the common greenhouse plants possess stomata on the upper surfaces. Weiss and others have collected considerable data showing the relative abundance of the stomata upon the different surfaces of dorsi-ventral leaves, from which the following examples may be suggestive: —

LEAVES WITH NO STOMATA ON THE UPPER SURFACES

PLANT	STOMATA PER SQ. MM. LOWER SURFACE
Abies balsamea (balsam fir)	228
Acer pseudoplatanus (Norway maple)	400
Anemone nemorosa (wind anemone)	67
Begonia coccinea (red begonia)	40
Berberis vulgaris (barberry)	229
Ficus elastica (rubber plant)	145
Juglans nigra (black walnut)	461
Lilium bulbiferum (lily)	62
Morus alba (white mulberry)	480
Ribes aureum (red currant)	145
Syringa vulgaris (lilac)	330
Tropæolum majus (nasturtium)	130

LEAVES WITH STOMATA RELATIVELY SCARCE ON UPPER SURFACES

PLANT	LOWER SURFACE	UPPER SURFACE
Asclepias incarnata (milkweed)	191	67
Cucurbita Pepo (pumpkin)	269	28
Lycopersicum esculentum (tomato)	130	12
Phaseolus vulgaris (bean)	281	40
Populus dilatata (poplar)	270	55
Solanum Dulcamara	263	60

LEAVES WITH STOMATA MORE NEARLY EQUAL ON BOTH SURFACES

PLANT	LOWER SURFACE	UPPER SURFACE
Avena sativa (oats)	{ 23 27	{ 25 48
Brassica oleracea (cabbage)	301	219
Helianthus annuus (sunflower)	325	175
Pinus sylvestris (pine)	71	50
Pisum sativum (garden pea)	216	101
Zea mays (corn)	{ 158 (68)	{ 94 (52)

LEAVES WITH MORE STOMATA ON UPPER SURFACES

PLANT	LOWER	UPPER
Nymphœa alba (water lily)	0	460
Pinus strobus (white pine)	0	142
Triticum sativum (wheat)	14	33

54. The effects of conditions upon stomatal production. — It has been indicated that the preceding data are suggestive. They do not, however, represent absolute relations, for the reason that the number of stomata is to a certain extent a factor of complex environmental conditions, varying with moisture-content of air or soil, light, temperature, and other conditions. In this connection some previously unpublished data[1] for corn and wheat grown under conditions similar except as to moisture-content of the soil may serve as an illustration. The plants were grown in tumblers of fine sand for seventeen days, and the counts of stomata are averages for the microscopic field employed (8 x ocular and 16 mm. objective).

CORN				WHEAT		
Per Cent of Water in Sand	No. Lvs. per Plant	Avg. Wt. of Tops	No. Stomata	Avg. Length of Tops	Avg. Wt. of Tops	No. Stomata
38	3.0	3.63	181	3.9	.46	103
30	3.0	3.54	130	6.4	1.09	85
20	3.0	3.36	129	4.7	.57	82
15	2.8	2.35	124	3.7	.35	81
11	2.0	1.56	107	3.7	.47	59

[1] These data are the results of experiments made by Mr. F. M. Harris in my laboratory.

The preceding table is sufficient to indicate that the number of stomata in a given area is variable. Again, there is no constant relation between the number in a given area and the size of the leaf; for, in the highest and lowest moisture-content with wheat, both length of leaves and entire weight of tops are approximately equal, yet in the low moisture-content there are only 57 per cent of the stomata found in the high moisture.

FIG. 27. Stoma of Helleborus: position of guard cells open (darker lines) and closed (lighter lines); cell contents shaded. [After Schwendener and Strasburger.]

55. The control of water-loss by stomatal movement. — The mechanism of stomatal movement has been abundantly studied. Commonly, wilting releases the tension which forces the guard cells apart, so that closure must be effected. Turgor of the guard and other cells of the stomatal region are therefore primarily important in determining the extent of the opening. The relative positions of the guard cells open and closed are shown in Figure 27, after Schwendener.

Recent studies upon the relation of stomatal movement to transpiration point to several suggestions and conclu-

sions of interest, although these studies also make it evident that there is yet much room for quantitative work in this field. In general, it may be said that, contrary to many early opinions, the stomata do not open and close in direct response to the varying conditions of the atmosphere which may inhibit or promote transpiration. When the plant is provided with sufficient moisture, the stomata are commonly open, but as Brown and Escombe and others have shown, maximum transpiration does not necessarily correspond with maximum opening. Wilting effects a closing of the pores, but according to Lloyd there can be no closing in anticipation of wilting. Again, the stomata may remain open when the humidity is extremely low, provided only sufficient water is available for the plant.

Many investigators have shown a primary relation between stomatal opening and the time of day; and it is believed that possibly through the possession of chlorophyll, and the relation to organic food-materials, there may be found in the turgor of these cells an important factor in stomatal regulation.

56. Modifications tending to check excessive transpiration. — Closure of the stomata is in all cases a means of checking the excessive transpiration, as already discussed. However, this check may be insufficient in extreme cases. It may prove also a menace to other activities of the plant. In any event many plants exhibit a structure peculiarly fitted to limit excessive transpiration. This is important in the occupancy by plants of arid habitats, and it is certain that many delicate species are unable to survive under conditions necessitating the most excessive transpiration. This may be due in part to the incapacity on

the part of such plants to respond to these conditions by the production of a protected surface or of growth-forms tending further to reduce the water-loss.

When transpiration is excessive, leaves commonly droop. This is an indication of wilting. It is usually regarded as a further protection against water-loss. At all events, such leaves obey an obvious physical law. The leaves of corn

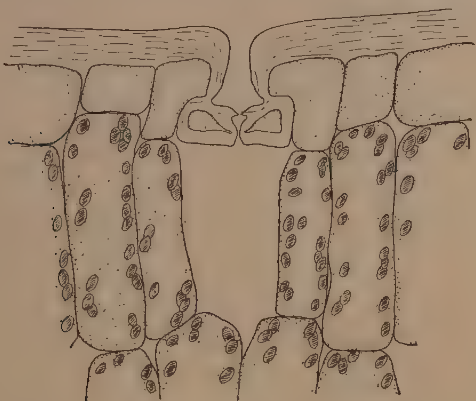


Fig. 28. Stomatal apparatus in leaf of carnation.

and some other plants "roll" under the same conditions. Here the tensions are different. It is often stated that in corn this rolling results because the stomata occur on the upper surface, but the data previously cited indicate that corn may exhibit more stomata on the lower than on the upper surface.

Plants which are commonly able to maintain themselves to advantage in arid situations may be modified in one or more of a variety of ways, some of which are as follows: —

(1) Reduced surfaces, such as in cactus, aloe, and many desert plants.

(2) Reduction in number of stomata, as in many grasses and sedges.

(3) Sinking of stomata in special epidermal cavities as in yucca and carnation.

(4) Thickened cuticle, as in carnation, pine, many desert plants, and the like.

(5) Production of a waxy bloom upon the cuticle, as in cabbage, sugar-cane, and wheat.

(6) The development of hairs upon the leaves, as in mullein and numerous mountain plants.

(7) The possession of water-storage tissues, as in many desert plants, begonia, etc.

57. Conditions affecting transpiration. — The conditions of the atmosphere greatly affect the evaporation from a water surface or from any other surface. In dry, hot weather, hay is quickly made and cured. The "pull" of the atmosphere upon all moist surfaces results, therefore, in a prompt loss of water. In the same way transpiration in a healthy plant is obviously influenced by conditions of the air, and it is to a certain extent influenced by conditions of the soil. In general, the important air factors are humidity, temperature, wind velocity, and light. Low humidity, high temperature, rapid movement of the wind, and intense light commonly facilitate transpiration

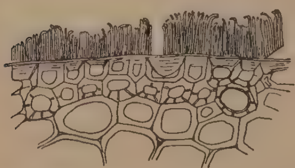


FIG. 29. From a stalk of sugar cane, epidermal region and "bloom" as a columnar deposit. [After De Bary.]

to a marked degree. In fact, if the water-supply is not abundant, a combination of these conditions may promptly result in wilting. The water-loss is not necessarily proportional to changes in conditions, since when transpiration becomes excessive, concentration of the cell-sap and the closure of the stomata exert, in many cases, a most important inhibiting effect, which is, in a way, protective.

The soil factors indirectly important in transpiration are water-supply and the strength or composition of the soil solution.

58. Effects of excessive evaporation. — The permanent effects of an excessive loss of water vary with the type of plant. Herbaceous annuals might quickly wilt and dry up. Deciduous perennials might be promptly defoliated. Many trees will show this during a summer drought, and if later wet weather prevails, there may be an entirely new season of growth. It is then comparable in effect to cold. Doubtless the excessive shedding of young flower-buds or "squares" of cotton is due to changes of the water relation. In general, reduced water-supply has a tendency to ripen up all parts, to mature seeds early, and often a considerable effect upon the composition of the product. Seeds ripened in this way are said to show the effects of immaturity, as shown later.

59. Guttation. — The elimination of water as liquid may occur in certain plants when absorption is promoted and transpiration checked. It consists in the forcible excretion through certain stomata of water which may collect as drops on the edges of the leaves or may stream down the leaf blades. It is conveniently observed upon young corn, blackberry, canna, and other plants. It may

occur during a cool afternoon or evening of a warm day; and quite commonly in the cool early morning after a hot day

[*Photograph by Russell and Harding.*]

FIG. 30. Destruction of cabbages by *Pseudomonas campestris*, a germ entering through the water-pores.

which has served to heat up the soil to a considerable depth.

The continuous water connection between the tissues and the external atmosphere established through guttation

makes possible the entrance of the germ of the black-rot disease to the cabbage and allied plants. This organism is productive of one of the severest of the cabbage diseases (Fig. 30).

60. Transpiration and evaporation. — Since transpiration is an evaporation phenomenon, it is possible to compare the amount of evaporation in different habitats, and thus be able better to determine or forecast plant behavior in such habitats. There are many difficulties involved in employing as a measure the evaporation of water from a freely exposed water-surface. The simple evaporimeter devised by Livingston is extremely satisfactory for this purpose (Fig. 31).

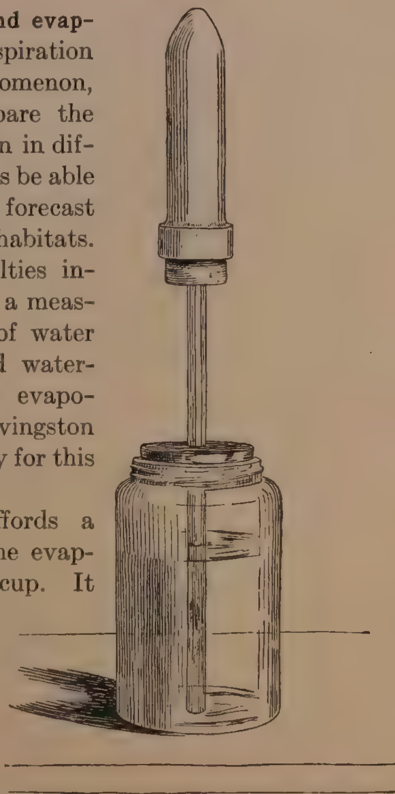


Fig. 31. Simple evaporimeter, Livingston form.

This instrument affords a means of measuring the evaporation from a porous cup. It consists merely of a bottle, or mason jar, through the well-paraffined stopper of which passes a tube connected by a rubber stopper with some type of porous cup

or filter tube, the whole being filled with water. This filter tube may be shellacked to a known surface, adopted as a unit, and all other instruments may be standardized with respect to this.[1] Under different conditions the curve of water-loss from this instrument may not be comparable to that from a free water-surface; but the effects of conditions upon it are supposed to be more nearly comparable to the effects upon plant surfaces.

The evaporimeter has also been serviceable in contrasting transpiration and evaporation in unit areas, thus relative transpiration may be taken as the ratio of transpiration to evaporation, conveniently expressed as $\frac{R}{E}$. The extent of variability respecting this ratio has been regarded a fair indication of what is conveniently termed physiological checking of transpiration. In studying this regulatory check upon transpiration Livingston finds that in certain desert plants it is especially operative between 6.30 A.M. and 1 P.M., and especially pronounced at temperatures from 79 to 90° F.

A proper study of the relation of certain horticultural plants to evaporation factors promises to yield much data of practical value.

Various observers have compared the loss of water from leaves with the loss from an equal surface area of soil. Nobbe has shown that evaporation from the surface of the soil may be 1.6 to 5 times the amount lost from an equal leaf area. In these cases the ordinary crop plants

[1] Transeau (*Bot. Gaz.*, **49**: 459, 1910) has recently constructed an instrument which seems to possess some advantages in the way of simplicity and rate of evaporation.

are considered. If, however, we should compare evaporation with the loss of water in such a plant as prickly pear (*Opuntia*), the former might be one hundred times as great. On the other hand, it should be remembered that a crop on a given plot may develop in leaf surface an area many times that of the soil upon which it is growing. Practically all direct measurements of the relative water-content of bare soil as contrasted with areas producing crops indicate that the percentage of water-loss is greater where a crop is grown. In other words, it is possible to conserve water in the soil by fallowing. The use of a fallow, together with sufficient cultivation to keep a constant surface mulch, is one of the first principles in dry-land farming.

King [1] has cited a case showing the effects of fallowing *versus* cropping, which is striking. Two plots which had been almost identical in water-content were used in the experiment. After the summer fallowing there was the next spring in the upper surface foot 9.35 pounds per square foot (or 203 tons per acre) more water than in the soil cropped the previous season. A considerable difference was still manifest after both plots had been cropped alike the succeeding season.

Practically, therefore, plants deprive the soil of moisture. It is well known that willows or birches in a moist spot in a yard or meadow keep the soil fresh and mellow. In some cases trees or other vegetation may seem to increase the soil moisture, but a closer examination will generally reveal the fact that in such instances the vegetation prevents rapid run-off and, therefore, appears to use the smaller quantity.

[1] King, F. H., "The Soil," pp. 291–292.

61. Transpiration and growth. — It has long been evident that there is, under certain circumstances, a relation or fairly definite ratio between transpiration and growth. As a result of various series of water cultures with wheat and other grasses, Livingston has attempted a further analysis of this relationship. He finds that the transpiration data are frequently as instructive as a comparison of total increase in weight or growth. It is observed, then, that transpiration and relative growth vary with weight and area of the leaves. The amount of transpiration is regarded as a simple function of the leaf surface, which again varies directly with leaf weight, or, practically speaking, with the weight of the entire tops. It follows, of course, that total transpiration is a more or less accurate measure of the total growth.

This relationship, however, is limited by several factors. It is necessary to have conditions favorable for fairly rapid transpiration and favorable for growth. Again, increasing the salt content of the solution in which plants are grown measurably affects transpiration and may not increase growth materially, so that plants growing in diverse concentrations may show extreme variations with respect to the amount of water-loss. Reed has also recently demonstrated that potassium in any combination exerts a depressing effect upon transpiration, while a small quantity of tannic acid facilitates it. In other words, the relation applies to a relatively narrow set of conditions.

62. Water transport. — This is a convenient but scarcely an accurate expression, since, except in the diffusion of water-vapor and in the formation of ice-crystals, there is, perhaps, within the plant no such thing as the

movement of pure water. In osmotic transfer water does move independently of substances in solution, but it is always associated with substances in solution.

The movement of water in the plant has been a line of experimental inquiry since the dawn of plant physiology. Many important facts have been clearly enunciated and numerous interesting data accumulated, yet some of the phenomena of movement observed find as yet no entirely satisfactory explanation. A chief source of difficulty lies in the complexity of the factors involved.

In general, however, diffusion is important, but the rise and maintenance of water are complicated by such factors as capillarity, the cohesive strength of water columns, the lifting power of evaporation, the peculiar structure of the conducting vessels, and, under certain conditions, the existence of high root pressures.

It has been stated that in the root the region of hair production is commonly characterized by a radial bundle arrangement apparently permitting more readily the movement of water from the parenchymal cells directly into the woody portion of the bundle. There is, of course, no such thing in plants as a true circulation, analogous to the circulation of the blood in animals; yet it is possible to distinguish in a very general way two types of movement in vascular plants, as indicated below.

(1) There is a "transpiration stream," from the absorbing organs (of water containing some salts and commonly traces of organic substances) to the leaves. This stream is directed mainly through vessels, the xylem part of the woody bundles (Fig. 32). During this transfer there is, moreover, general diffusion to all parts requiring

water, or possessing a sufficient tension therefor. From what has been said of water-loss and of the principles of diffusion it will be apparent that the type of movement

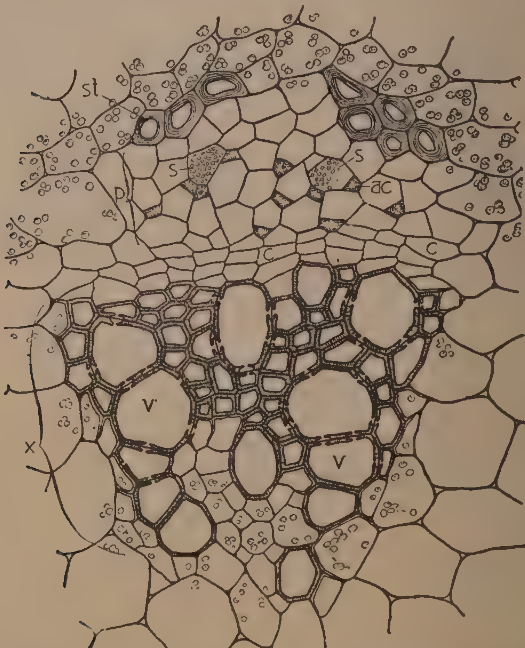


FIG. 32. Cross-section of primary fibrovascular bundle of Ricinus: phloëm (*P*), showing sieve tubes (*S*), companion cells (*AC*), parenchyma and sclerenchyma; cambium (*C*); and xylem (*X*), showing especially vessels (*V*) and tracheids. [After Curtis.]

here discussed is more than diffusion. Moreover, rapid movement is essential in order to supply the demands of transpiration, and it is this transpiration stream which

effects, for one thing, perhaps, a rapid distribution of absorbed mineral nutrients.

On the other hand there is (2) a more gradual movement by diffusion of soluble organic materials, or "elaborated" foods, along the paths provided by the plasmatically connected sieve tubes (Fig. 33), from which general paths

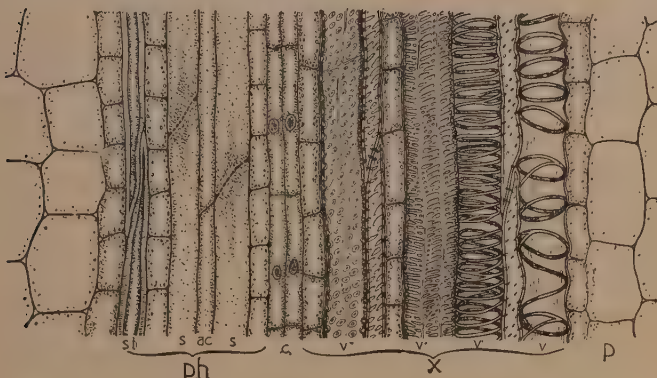


FIG. 33. Longitudinal section of a bundle similar to the preceding. [After Curtis.]

organic substances pass, also by diffusion, into all cells where growth and differentiation are proceeding. At certain seasons, in many plants during the spring, the movement of organic material in the xylem part of the bundles is common. Usually, however, the distinction may be made that the dead vessels or xylem elements conduct a liquid which is more nearly the nutrient solution absorbed from the soil, whereas the sieve-tube part of the bundle is primarily the path of diffusion for organic materials. All cells of the body—parenchyma, cortex,

and the like — permit of diffusion, and in the end the demands of each cell govern the flow toward that cell.

63. Fibrovascular bundles. — If freshly cut (under water) shoots of the jewel-weed, sunflower, Indian corn, canna, or other convenient representatives of monocotylous and dicotylous plants are placed in a solution of a dye such as eosin or fuchsin, the stain will pass upward through the conducting system of the plant, and the paths of conduction may thus be made evident, although there is sometimes a slight lateral diffusion tending to obscure the definite channels.

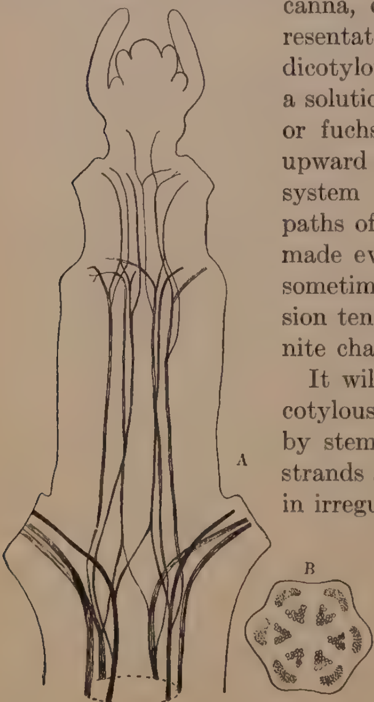


FIG. 34. Vascular system of Clematis, apical portion of the stem: longitudinal view of stem and leaf trace bundles (*A*), and cross-section of internode (*B*). [After De Bary and Nägeli.]

It will be recalled that monocotylous plants are characterized by stems in which the vascular strands are commonly distributed in irregular manner throughout a ground tissue called parenchyma, as in corn or sorghum. A hand section will show at a glance this distribution of the bundles, and it is also strikingly brought out by breaking a dry corn stalk through an internode

and noting the strands. Examined microscopically a bundle exhibits in cross section the typical collateral arrangement. In this the phloëm or sieve-tube part is outermost, the xylem therefore within, and both are generally inclosed by a sheath of stereome or mechanical supporting tissue. There is, however, no meristem or cambium within the bundle, signifying a closed type. The irregular distribution of bundles in the stem usually precludes the formation of a ring of wood, and there is, moreover, no bark in the usual sense. These are matters of much physiological significance, both from the standpoint of growth and conduction.

In dicotylous plants the primary bundles are arranged in a ring and are also commonly collateral. The interposition of secondary bundles (as subsequently discussed, section 187) may result in the formation of a complete wood-ring. Where no wood-ring is produced, the bundles run parallel throughout much of the internode (Fig. 34), divide and unite in a characteristic fashion at or near all of the nodes, also sending off branches to the leaves at each node.

When a wood-ring is produced in a dicotylous stem, the meristem of the bundles forms a continuous growing layer, the outer portion of the wood-ring then consists of phloëm and the inner portion of xylem. The cambium between permits the addition of seasonal or growth rings of phloëm and xylem on the outer and inner sides respectively. In plants which attain a considerable age the parenchyma accompanying the bundles loses its protoplasm and the bundles cease entirely to take part in conduction. The number of rings of new wood which may be active in conduction varies greatly with different plants.

64. Leaf venation. — Each leaf receives a definite quota of bundles, and these and their subdivisions continued into petiole and lamina constitute the so-called venation system. In the case of monocotylous plants the veins are usually parallel from the leaf stalk, or from the mid-vein, so that they are often designated parallel-veined plants.

In the leaves of the dicotylous type the bundle systems branch repeatedly, and also form a complete reticulum.

[*Photograph by H. M. Benedict.*]

FIG. 35. Minute venation of the leaf of *Vitis riparia*; leaves of different ages.

In any event the leaves are well provided with fibrovascular tissue, easily demonstrated by macroscopic or microscopic observation. As a matter of fact the bundles extend to the most remote parts, and in dicotylous plants especially the leaf is divided up into a complete network, with the areas between the vascular tissue being seldom larger than 1–3 mm. in diameter (Fig. 35). The ultimate subdivisions of the bundles consist of tracheids and elongate parenchyma cells (meristem). Sometimes the bundles end abruptly or blindly. As the leaf grows each area subtended by veinlets becomes larger, and this increase

in size may be followed by the laying down of new veinlets of a lower order (at first fewer tracheids) from each side of the original space. These may be at first procambial in nature, but tracheids are rapidly differentiated within. It is of special interest to note that the sieve tubes disappear relatively early in the minute continuations of the bundles.

65. **Rate of transport.** — The rate of transport of water in the fibrovascular bundles may be determined with a fair degree of accuracy by means of the rise of dyestuffs as before noted, but more accurately in many cases by the method of Sachs, wherein lithium nitrate is used in the solution and its presence after intervals determined by burning the tissues and examining the flame spectroscopically. According to Sachs the rate of water rise is extremely diverse, and may vary from a few centimeters per hour to one or more meters. Doubtless the extremes are often greater than these indicated, but unquestionably the difficulties of measurement are greater at the extremes.

LABORATORY WORK

Indication of transpiration. — Stahl's cobalt test may be employed to determine water-loss from a plant surface. Incidentally it determines roughly the presence or absence of stomata, or the relative abundance upon the upper and lower surfaces of the leaf. Soak filter paper in a 5 per cent solution of cobalt chloride, dry in the oven or over a flame, and note the blue color. Breathe upon a small piece of this paper and note that the absorption of moisture induces a change to pink. Now cut out two pieces of the paper of equal size; place one upon the upper and one upon the lower side of the leaf to be tested, cover each with a piece of mica and cement the latter

to the leaf with plasticene or prepared wax. In this experiment handle the paper with forceps, and preferably use a leaf attached to the plant, or a shoot, the stem of which is immersed in water. Note any change of color, and the time required to produce change, in the two pieces. Experiment with several of the plants mentioned in section 53, and contrast your data with the indications regarding stomata there furnished.

Amount of transpiration, determined by weight. — The actual transpiration of potted plants may be carefully determined by loss of weight, as already indicated. Employ plants of any kind convenient, preferably one-stemmed plants with large, relatively simple leaves; inclose the pot in soft rubber cloth, in aluminium shells and rubber cloth, or in any manner convenient to prevent evaporation from the pot and soil, the plant being previously watered. Weigh carefully and repeat the weighing after each of several intervals of not more than twelve hours. If water is again applied, add approximately the quantity lost, and weigh again. Plot the results. This experiment may be extended through a considerable period of time, and different types of plants may be contrasted. Ultimately, the area of each plant must be taken into consideration or unit areas compared, as indicated in later experiments.

The transpiration of plants grown in water cultures in paraffined wire baskets, or in glazed pots covered with paraffin, is also conveniently determined by weighing, as referred to in subsequent sections of this book.

Measurement of leaf areas. — It would be difficult to determine directly the transpiration of a tree or of any vegetation under natural conditions. For the laboratory experimental work in contrasting different plants or plants under different conditions, as well as for an indication helpful in estimating water-loss in the field, it is desirable to have a quick method of measuring leaf areas.

Many methods of determining leaf areas are now used. Ordinarily it is sufficient to trace the outline of the leaf upon coördinate paper, the area being determined by a count of spaces. Another simple method is to trace the outlines of the leaves

employed (or of average leaves) upon paper of uniform thickness, these outlines being subsequently cut out and weighed accurately for comparison with the weight of a known area. Prints may be made upon sensitized paper, or the planimeter may be employed. The area of stems and petioles is generally negligible, but may be roughly estimated when necessary. It is well to express all transpiration data, as suggested by Ganong, in grams per hour per square meter of surface, written $g\ m^2\ h$.

Amount of transpiration, determined by potometers. — Set up a transpiration experiment, employing either the Ganong potometer (Fig. 24), a burette potometer (Fig. 23), or some other form equally satisfactory. The former may be employed for short periods, contrasting the effect of conditions; while the short burette potometer may be used for longer intervals, care being taken, however, to keep the column of water in the burette at a height approximately equal to that in the other arm.[1]

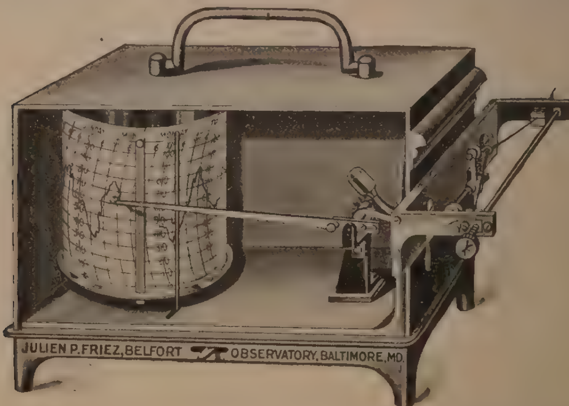
Effects of conditions upon transpiration. — It has been indicated that temperature, humidity, air movement, etc., are directly and indirectly important in varying transpiration quantities. While the effect of light variation may be demonstrated, more satisfactory experiments may be made with the other factors.

A rough idea of the effects of temperature and humidity may be obtained by simple transpiration experiments with simultaneous observations upon simple thermometers and hygrometers, placing plants of more or less equivalent areas, even for a few hours, under conditions determined to be diverse. With more or less equal lighting, contrast the transpiration, for example, in a moist basement room with that in a warm upper room; or, at a uniform temperature, also, contrast a plant exposed in a quiet room with one in the same room under a large bell glass, the latter securing greater humidity. Diverse con-

[1] In all transpiration or other experiments where the further absorption of water by excised shoots is required, the cutting of the shoot should be done while it is bent under water, and the ends of the shoots should be promptly immersed in water until used.

ditions may also be obtained in different greenhouses. Keep an accurate record of the conditions of the experiments, and accompany this with a record of the transpiration data, expressing the latter in terms of $g\ m^2\ h$, as above explained.

A more accurate evaluation of the factors, and consequently a better conception of the effects of external conditions upon plants, may be obtained by means of experiments continued several days, whilst utilizing, also, autographic recording instruments. Study the mechanism of the thermograph (Fig. 112) and hygrograph (Fig. 36); also set up and standardize some simple evaporimeters (Fig. 31) after the method of Livingston



[*Illustration from Julien P. Friez.*]

FIG. 36. Hygrograph.

(section 60) or of Transeau (*Bot. Gaz.*, **49**: 459, 1910). Then set up in duplicate with the burette potometers a transpiration experiment (preferably two, under two sets of conditions). This is to be accompanied by the continuous record of temperature and humidity. Make observations upon water-loss as often as possible. The experiment may be continued several days if shoots with woody stems are chosen. Plot and discuss the results.

Under conditions otherwise similar place one plant (or potometer) and a standardized evaporimeter in a current of air (an electric fan may be employed), and a similar plant and instrument in a quiet atmosphere. Contrast the water-loss after a sufficient interval.

Guttation. — Water freely some potted plants of cabbage or corn with warm water until the temperature of the soil is about 35°; then transfer the pots promptly to a cool room, cover with bell glasses, and after a few hours describe any exudation phenomena noted.

Leaf structure. — Make hand sections of a variety of leaves (at least four types) and compare by microscopic study, especially the epidermis, palisade tissue, and intercellular spaces. The following leaves are suggested: beech, cherry, or ivy; rubber plant or rhododendron; snap-dragon or jewel-weed; carnation or small cereal; pine or spruce. Draw in detail one type.

Examine and compare, if possible, leaves of any variety of small cereal grown under diverse water conditions. Note especially, the width and venation of the leaf, the amount of bloom, and the number and distribution of the stomata.

Conduction of water. — Cut under water several shoots of young sunflowers, castor-oil plants, jewel-weed, corn, and some plants with light-colored flowers (hyacinth, phlox, or other herbaceous plant convenient), and place the cut ends in vessels containing a red dye. After the lapse of an hour or two note the course of the dye through the stem, also into the leaves and petals. With long standing is there more general diffusion of the dye? Describe the results.

Remove shoots which have been in the dye for a very short period (15 minutes to 1 hour), wipe off the surplus dye from the outside with filter paper, and with a sharp knife or razor cut off the stem and examine promptly with the hand lens to ascertain what portion of the bundle is colored. In the case of the sunflower and castor-oil plant is the entire ring colored? Peel off the bark of the dicotylous plants and examine it for the dye. Draw conclusions.

The rate of movement may be studied by leaving the shoots from half an hour to one hour in the dye, then cutting off the stems at successive intervals until the uppermost indication of the stain is found, through examination with a hand lens. After determining the rate of rise of the liquid at laboratory temperature, place some shoots under conditions favorable for rapid transpiration and others under a bell glass, and contrast the results. According to the directions in the next paragraph [1] decolorize a leaf of the grape, sunflower, or fuchsia, and under the low power of the microscope study the minute ramifications of the veins.

Place fresh tissue in equal parts of 95 per cent alcohol and glacial acetic acid. After from 24 to 48 hours, take pieces and hold them immersed in pure nitric acid until clear (usually a matter of seconds), place on a slide, add glycerin, and boil over flame until tissue becomes entirely transparent. Put on cover glass and examine in the glycerin.

Ring small plants such as geranium, sunflower, Ricinus, or other forms with definite bark, by removing a circle of bark about one fifth of an inch long, extending completely around the stem. The plants should not be in an atmosphere so extreme as to cause rapid drying-out from the cut surface. Does ringing interfere with the conduction of water to the leaves?

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[1] A method suggested by Professor H. M. Benedict, University of Cincinnati.

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Texts. *Barnes*, *Detmer*, *Ganong*, *Goodale*, *Jost*, *Pfeffer*, *Stevens*.

CHAPTER VI

THE WATER REQUIREMENTS OF CROPS AND OF VEGETATION

FROM what has been said respecting the use of water by plants, more especially transpiration, it is obvious that the requirements of vegetation and of crops will be most diverse, and that any particular crop or type of vegetation will show a modified use dependent upon temperature, light intensity, strength of soil solution, texture of soil, and the like.

66. Relative requirements of a few crops. — Lyon and Fippin have compiled a statement of the water needs of several crops which is suggestive. These crops were tested by the different observers under dissimilar conditions, and close agreement is not to be expected. Moreover, the methods of controlling or estimating the evaporation of water from the surface of the soil has not been the same with the different observers, and this might easily lead to important differences. See table on opposite page.

Taking 300 pounds of water as an average amount transpired by crop plants, in order to produce 1 pound of dry matter under conditions in England, Hall has prepared a table giving the precipitation necessary to supply the water used by certain crops. For conditions in the central

WATER TRANSPIRED BY GROWING PLANTS FOR ONE PART OF DRY MATTER PRODUCED

Estimations made by							
Lawes and Gilbert, England		Hellriegel, Germany		Wollny, Germany		King, Wisconsin	
Beans	214	Beans	262	Maize	233	Maize	272
Wheat	225	Wheat	359	Millet	416	Potatoes	423
Peas	235	Peas	292	Peas	479	Peas	447
Red clover	249	Red clover	330	Rape	912	Red clover	453
Barley	262	Barley	310	Barley	774	Barley	393
		Oats	402	Oats	665	Oats	557
		Buck-wheat	371	Buck-wheat	664		
		Lupine	373	Mustard	843		
		Rye	377	Sunflower	490		
Average	237		341		608		424

United States it would be more nearly accurate to assume an average requirement according to King's results of about 425 pounds of water for each pound of dry matter. Modifying the data in accordance with this, the indications are as follows: —

Crop	Wt. at Harvest	Per Cent of Water	Wt. of Dry Matter at Harvest	Calc. Water used during Growth	
	Tons per A.		Tons per A.	Tons per A.	In. of rain
Wheat	2.5	18	2.05	922.5	9.13
Barley	2.0	17	1.66	747	9.39
Oats	2.5	16	2.10	945	9.36
Meadow hay	1.5	16	1.26	567	5.61
Clover hay	2.0	16	1.68	756	7.48
Swedes	17.0	88	2.04	918	9.09
Mangolds	30.0	88	3.60	1620	16.03
Potatoes	7.5	75	1.87	841.5	8.32
Beans	2.0	17	1.66	747	7.41

In all cases the amount of water given is a considerable part (averaging about one fifth in the central United States) of the annual rainfall. Considering the run-off and the evaporation from the soil, both during and outside of the growing season, it is essential to study carefully the water requirements of crops, even in regions where the rainfall seems generally adequate.

An abundant or optimum supply of water in part obviates the necessity of maximum cultivation, since cultivation may be very considerably concerned with conservation of water. Nevertheless, there are factors of aëration, proper conditions for certain types of bacterial action, texture of soil, and the like which require cultivation, wholly aside from the water relation.

67. Precipitation and crop growth. — Under ordinary circumstances the greater part of the precipitation water is not conserved by the soil. Of the total annual rainfall only a certain percentage is available to vegetation or to the crop. Some of the water is lost in the immediate surface run-off, a small part may be lost by percolation, and there is further a considerable amount represented by evaporation. When the water-table is low, plants are, of course, wholly dependent upon the water which is conserved in relatively superficial strata.

Practically speaking, no section of Europe or of the United States is wholly free from droughty periods. This implies the well-recognized fact that precipitation during the growing season is demanded by the great majority of crops and types of vegetation. Nevertheless, when proper measures are taken for the conservation of water which may fall outside of (as well as during) the growing

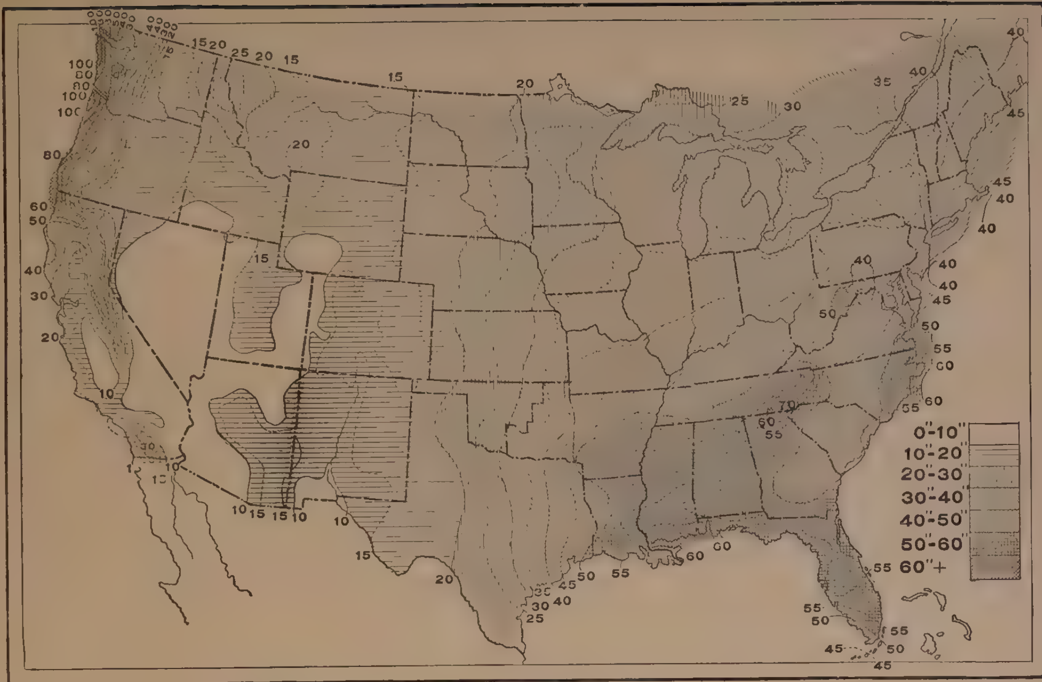

Fig. 37. Mean annual precipitation in the United States.

season, a relatively small precipitation — say 25 to 30 inches — may be sufficient for crop production. Early maturing grains and other grasses require as little, perhaps, as any other type of vegetation affording an equal yield.

A chief cause of the annual variation in yield of many staple crops is to be found in the variation in rainfall. Smith has prepared charts showing a remarkable agreement between yield of corn and precipitation in the corn belt of the United States for the chief growing months — June, July, and August. In Figure 38 the dotted line gives the average rainfall for the months mentioned, covering a period of fifteen years, and the full line gives yield of grain per acre for the same time. The data are taken from Ohio, Indiana, Illinois, Iowa, Nebraska, Kansas, Missouri, and Kentucky.

The chart (Fig. 37) shows a rainfall map of the United States for a period including, in the main, the growing season. From this, it is apparent that the rainfall west of the hundredth meridian practically to the Coast Range valleys of the Pacific is less than the usual requirement, and so the number of crops which may be grown in this general region without irrigation is extremely limited. In fact, throughout a very large portion of western North America, eastern and southern Europe, northern Africa, and a large part of Asia and Australia, crop production is limited much more by insufficient or ill-distributed rainfall than by all other factors combined.

It is believed that the great agricultural countries of the world must be, in time, those of great area, such as Australia, Brazil, China, India, Russia, and the United States. In three of these, however (China, India, and

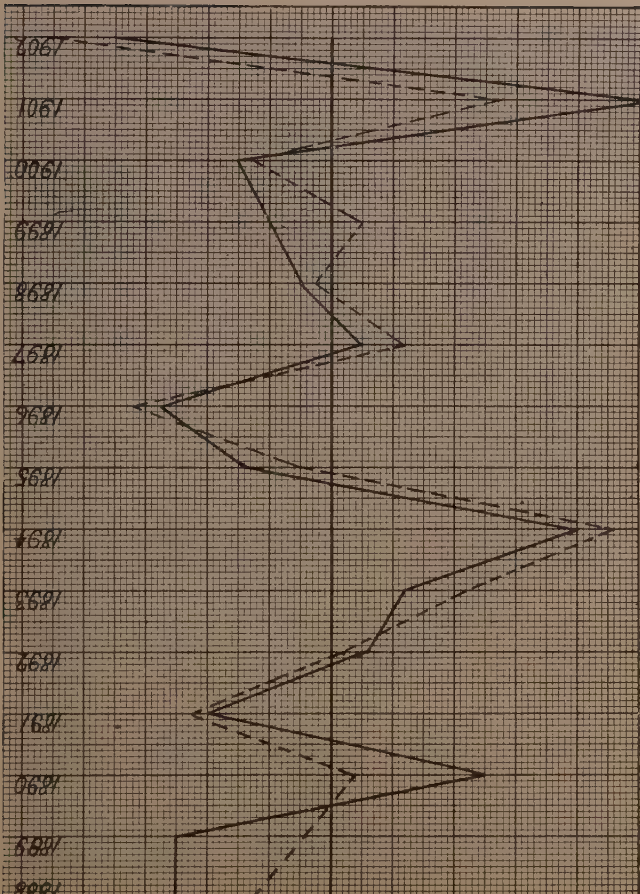

FIG. 38. Precipitation (heavy line) for June, July, and August in the corn belt of the United States, and yield per acre (broken line). [After Bureau of Soils, U. S. Dept. Agl.] [Major ordinates (10 spaces) denote 1 bu. yield and 2 ins. precipitation.]

Russia), famines may be expected any year when the rainfall is but slightly less than usual, and without their fairly well-developed systems of irrigation much larger areas of these countries would remain in doubt with respect to production. Where irrigation is not practiced, it is frequently necessary to introduce systems of dry-land farming whereby the principles of soil-moisture conservation are effectively applied, and sometimes a single crop is grown in two years, water being allowed to accumulate every second year.

Precipitation has a maximum effect, of course, when all conditions are favorable; that is, when the nature of the soil and its depth, the type of sub-soil, the slope and exposure of the ground, all combine to conserve moisture and deliver it to the growing crop.

68. Irrigation. — Both in Europe and America (in many sections where irrigation has not been considered necessary) it has now been abundantly demonstrated that the yield of most crops may be materially increased by a rational use of water. In Wisconsin, for example, King[1] has found that during a six-year period the yield of potatoes was increased from 217.3 bushels to 301.7 bushels per acre. Again, with twelve inches of rainfall during a growing season for corn, the yield of grain was increased by means of irrigation from 30.14 to 65.3 bushels.

It has already been indicated that profitable crop production is only possible in many regions when irrigation practices supplement the effect of the normal rainfall. In every drainage basin, large or small, there are opportunities for conservation.

[1] King, F. H., Wis. Agl. Exp. Sta. Report, **18**: 195, 1901.

FIG. 39. Rice-field prior to drawing off water for harvesting, Louisiana.

Fruits. — In most sections of the Pacific coast region, deciduous fruits are commonly irrigated when the rainfall is less than twenty inches, and many believe that irrigation may be desirable when the precipitation is equal to or somewhat greater than this amount. Citrus fruits grown on a commercial scale in that region are invariably irrigated. In all cases the purpose of irrigation, as Wickson says, " is a means of soil improvement to be employed, like other means of improvement, when the soil needs it."

The following tables will suffice to indicate for the two types of fruit mentioned the usual amount of water added by irrigation to supplement the normal precipitation: —

Deciduous Fruits

	Rainfall in In.	Irrig. Season	No. Irrig.	Each Irrig. In.	Total Irrig. In.
Sacramento . .	18–20	June to October	3–18	1–1.25	3.25–18
Santa Clara . .	12–20	Spring, summer, or winter	1– 3	3–12	12–16
Fresno . . .	8	Summer or winter	1– 4	2.5–12	7.5–12
Los Angeles . .	12–20	Spring or summer	1– 3	2–9	4–9

Citrus Fruits

	Rainfall in In.	Irrig. Season	No. Irrig.	Each Irrig. In.	Total Irrig. In.
Fresno . . .	8	April to October	2–7	2	4–14
Los Angeles . .	10–20	March to November	3–7	1–9	3–27
San Bernardino .	12	March to December	4–8	1.5–6	6–36
Riverside . . .	7–12	When needed, or April to December	3–9	1.5–6	10–36
Orange . . .	10–18	When needed, or March to December	3–8	2–5	10–40
Tulare . . .	10	March to October	5–10	2.6	12–60

Corn. — The period of growth of this plant is long, and in temperate regions it extends throughout the warmest season. The water requirements are considerable; consequently in semiarid or dry regions it responds abundantly to proper irrigation. The most striking re-

sults have been secured at the Utah Experiment Station. In the table below there are included the data respecting yield, and also the effect upon protein content: —

Irrig. Water In. Applied	Yield of Grain per A., Bu.	Protein in Water-free Substance, Per Cent
38.00	82.71	12.99
36.53	69.28	12.05
19.98	77.00	13.00
19.97	49.28	12.65
15.00	46.28	13.17
15.00	58.71	13.79
10.00	56.86	13.42
7.50	35.14	15.08
0.00	26.00	14.52

Wheat. — In comparison with the data given for corn with different amounts of irrigation, it is of interest to examine the results secured at the same station with wheat. The accompanying table indicates not only the amount of

Water Applied, In.	Yield per Acre, Bu.	Percentage of Protein in Grain	Percentage of Ash in Grain	Yield (in Pounds) per Acre of Nitrogen	Yield (in Pounds) per Acre of Ash
4.63	4.50	24.8	2.50	10.7	6.75
5.14	3.83	23.2	3.07	8.5	70.5
8.73	10.33	19.9	2.54	19.7	15.74
8.89	11.33	19.4	2.93	21.1	19.72
10.30	14.66	18.4	2.34	25.9	20.24
12.09	11.16	21.3	3.25	22.8	21.44
12.18	11.66	23.1	2.88	25.8	20.30
12.80	13.00	17.1	2.52	21.3	21.50
17.50	15.33	17.2	2.57	25.3	23.64
21.11	17.33	15.9	2.34	26.4	24.33
30.00	26.66	14.0	4.14	35.8	26.20
40.00	14.50	17.1	2.52	23.8	21.92

water supplied and the resulting yield, but also the protein and ash content of the grain and the total amount of these components (protein as N) taken from the soil.

From the preceding table it is evident that, in general,

FIG. 40. Springs and reservoir for irrigation of date-palms, Figuig, Morocco.

irrigation water up to thirty acre inches increased the yield of grain and diminished the nitrogen content. The effect of an increase of over thirty inches of water is greatly to diminish the yield; but the percentage, the composition, and the total removal of soil constituents per acre remain

practically the same as when one third as much water was supplied.

Date-palm. — In the Saharan region of northern Africa, where the date-palm is most extensively grown, the precipitation is commonly less than ten inches. Moreover, during the growing season the air is intensely dry, and evaporation reaches a maximum. Under such conditions, and assuming no subterranean water-supply, it has been estimated [1] that this plant (a tree of medium size) requires a maximum of from 100 to 190 gallons of water per day during at least four months, making a total of from $3\frac{1}{2}$ to $4\frac{1}{2}$ feet of irrigation-water annually.

69. Potted plants and water supply. — Potted plants possess such diverse water requirements that it is often difficult for the amateur grower to arrive at any satisfactory principles for watering. First of all, it is clear that the amount given should be in proportion to the water-loss. Plants in a dry room or greenhouse may require many times as much water as those in a shaded greenhouse full of vegetation, with air fairly saturated. Most potted plants are quickly injured or killed by constant saturation, and the practice of saturating the pot and filling the jardinière around it is soon fatal; for with the usual amount of organic matter in the soil the exclusion of air to this extent is harmful both directly and indirectly.

Viewing this matter in the light of such experimental work as has been undertaken, it seems that during the growing season a constant, favorable supply of water from below is most desirable. This, of course, is not always

[1] Swingle, W. T., "The Date-palm." Bur. Plant Ind., U. S. Dept. Agl., Bul. 53 (cf. pp. 47–48), 1900.

practicable, but it serves to emphasize the fact that alternate flooding and drying is not necessarily ideal. The latter is far better than stagnation. When in vigorous growth, the plant suffers from drying-out, and some part of the absorbing surface is killed every time the soil becomes air-dry.

In general, there is a certain relation between abundant water-supply and vegetative growth, so that it may be necessary to check watering somewhat to induce more abundant flowering. Again, in the case of plants which flower periodically, it may be desirable, or even imperative, to permit the plant to pass into a resting or semidormant condition. If the plant as a whole is to remain alive, water may not be entirely withheld, but in the case of many bulbous and fleshy-rooted plants it may be highly desirable that all other vegetative organs disappear, and coincidently it may be desirable that all other conditions favoring metabolism (such as high temperature) may be reduced.

The cultivation of plants whose peculiar growth-forms are dependent upon dryness of habitat is a special case, just as is the cultivation of water plants, and some of the general relations of these types are subsequently treated.

70. Ecological classification based upon the water relation. — In the previous paragraphs of this chapter plants of the most diverse water relations have been discussed; those of the desert represent one extreme and those of ponds and water-courses the other, between which extremes falls the great majority of plants. The water relation was recognized by Warming to be most important in attempting a habitat or ecological classification of forms. With respect to this factor he has made from the natural

intergrading series of forms three primary groups which are conveniently designated (1) xerophytes, (2) mesophytes, and (3) hydrophytes.

Xerophytes. — Plants adjusted to physiological dryness are properly termed xerophytes. In the preceding pages references have been made to the fact that there are a large number of plants both perennial and annual which are able to exist in typical desert situations. In general, such plants are tough, often hairy, and they usually possess reduced or leathery leaves. Accompanying these modifications there may be histological adjustments which may serve to check water-loss during the more arid periods, and to accumulate or store water when it is more plentiful. Special peculiarities of the epidermis, and of the plant in general, as affecting transpiration, have been discussed. The cactus, yucca, and sage-brush of the southwest are plants possessing the capacity for types of modifications which enable them to persist and to become the dominant vegetation in much of that region.

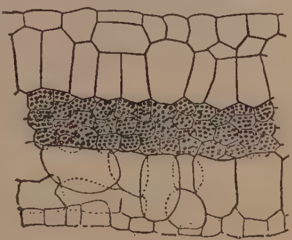

Fig. 41. Section of Begonia leaf, showing colorless water-storage tissue adjacent to epidermis. [After Coulter.]

Some of the most famous writing papers are those manufactured in Scotland and England from a widely distributed and much exploited African desert grass known as alfa. This name refers particularly to *Stipa tenacissima*, which occupies millions of acres in the steppes of northern Algeria. It is a plant too tough even to furnish food for

FIG. 42. Vegetation of semiarid sand hills, eastern Colorado, especially *Artemisia filifolia* (Sand-sage). [Photograph by H. L. Shantz.]

the camel, and it thrives under conditions which would perhaps eliminate the great majority of the grass species of the semiarid United States.

Mesophytes. — The mesophytes occupy an intermediate position with respect to water requirements. They constitute therefore the chief elements of the terrestrial flora, and in fact the main crops and herbaceous vegetation of the earth. Likewise the species constituting the typical forests of northern Europe and America, as well as most of those of tropical regions, would be classed in this category. In other words, we have in this group a great majority of those plants which constitute crops in the usual sense of this term. The relative abundance of plants requiring an intermediate amount of water results in a tendency to consider them as the normal plants, whereas others may be regarded as abnormal, or as specially adjusted to persistence under intensified conditions.

Hydrophytes. — All plants growing wholly or partially submerged are denoted hydrophytes. Typical members of this group, such as the water lilies, or water millfoil, exhibit modifications of structure which are of much interest. It is important to refer again to the fact that soil water is not pure, and must of necessity contain substances in solution. The water of most streams, ponds, and inland lakes contains relatively small quantities of organic matter, and invariably small amounts of many mineral compounds; such fresh waters support one type of vegetation. Ponds which are common in the typical bog regions of the northeastern United States and elsewhere may contain organic materials produced under peculiar conditions, which apparently serve to make the

water less valuable physiologically. Any tendency in this direction results in a similar inclination to xerophytism in the flora which may occupy these waters. From the standpoint of the relations of vegetation in general, the water of the sea is to be regarded as almost unavailable physiologically, on account of the large content of salt which it contains. Flowering plants which grow in salt marshes are often, therefore, typical xerophytes.

71. Semi-xerophytism and hard-wheat production. — The hard-wheats are species or varieties which, for the perfection of their particular economic qualities, require a relatively small water-supply. They are the varieties now cultivated in much of the Central West immediately west of the hundredth meridian. In this section the precipitation during the growing season is so inadequate as distinctly to shorten the growing period. This is, moreover, emphasized by the high temperature of the summer season. Other factors may play a part, but in general the growing season is determined by the conditions mentioned.

This shortening of the growing season is apparently wholly comparable to incomplete maturity. The hard-wheats have a tendency to produce high nitrogen content, and immaturity accentuates the relative increase in protein material and sometimes seems even to augment the total absorption of nitrogen. At any rate, in high nitrogen content, or gluten, lies the advantage of these wheats for semolina and other purposes (including bread-making) to which they are put, so that there exists an interesting relation of region to product.

The hard-wheats have, for the most part, originated under conditions more or less similar to those prevailing

in the West, and the introduction of these varieties has greatly increased crop production and the possibilities of

FIG. 43. Semiarid sandhills of eastern Colorado; *Andropogon scoparius* (bunch grass) and *Bouteloua hirsuta*. [Photograph by H. L. Shantz.]

agriculture. These wheats are apparently adjusted structurally to absorb more water, by increased root development, and to conserve it better, by lessened transpiration.

They also mature early, ripening before the conditions are such as to prevent development, and finally, they are able to adjust themselves more or less to considerable changes within the growing period.

The following summary, adapted from Lyon, may therefore indicate the conditions under which hard-wheat production may be maintained: —

(1) A relatively dry atmosphere which emphasizes the drought conditions.

(2) A short growing period, which is equivalent to early maturity and is unfavorable to starch-storage in the later stages of growth.

(3) A favorable nitrogen supply in available form.

It may be readily inferred that if certain of these conditions do not naturally obtain, or if they are artificially changed, there may be a tendency to make softer wheats of the hard varieties. From experiments in Washington (Thatcher), it has been shown that the total precipitation in the different counties of the state governs very closely the composition of the kernel; therefore, as under irrigation, there is here a tendency — with higher precipitation — to produce the characters of soft-wheat where otherwise a hard-wheat would be developed.

SUBSIDIARY WORK

Students not taking work directly along agricultural lines may be required to prepare a report upon some phase of the water requirements directly related to drainage, some aspect of irrigation, or the water-relations of special crops, utilizing any accessible literature. Agricultural students, less likely to consider adequately the ecological aspects of vegetation, may be given a

topic requiring some careful study in Schimper and Warming, or a critical analysis of any special articles available.

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CHAPTER VII

MINERAL NUTRIENTS

In a physiological sense the common fertilizers, or "artificial" fertilizers, sold upon the markets of a large part of the world are, with respect to plants, soil nutrients or amendments. A study of fertilizers and of conditions and factors governing the use of these under diverse field conditions constitutes a special phase of agronomic or soils work. At all points this field of work overlaps physiological inquiry, for ultimately the plant response, or yield, is the index to favorable or unfavorable soil condition. But the most significant fact is that in his most important work the agronomist usually deals with these problems in such a complex form that it is not possible to analyze the result in terms of direct plant response. Just as the agronomist's work is important, however, in securing such general results, that of the physiologist is important in the attempt to simplify conditions, to analyze factors, and ultimately to determine the nature of the plant response.

72. The ash content of plants. — It has been noted that water constitutes ordinarily about four fifths of the weight of herbaceous plants. The remainder is solid matter. When the latter is burned in an open fire, the organic products are volatilized, and most of the mineral

constituents remain in the ashes (technically the ash). Water, total solid matter, and ash are therefore readily determined by simple methods.

The total ash seldom amounts to more than 2 or 3 per cent of the green-weight, and any single mineral element of this ash constitutes, as a rule, merely a fraction of 1 per cent of the weight of the plant; yet every essential mineral element is quite as important as any other factor in plant production. The percentages of ash in some familiar plants and plant products are given in the following table:[1] —

Product	Total Solids	Ash, Per Cent of Total Product	Ash, Per Cent in Water-free Substance
Corn, green fodder	20.67	1.16	5.6
Corn, ripe grain	89.44	1.53	1.7
Sorghum, green fodder	20.60	1.09	5.3
Wheat, ripe grain	89.48	1.87	2.0
Timothy, green hay	38.42	2.10	5.4
Red clover, green hay	29.21	2.10	7.2
Red clover, cured hay	84.76	6.15	7.3
Alfalfa, green hay	28.25	2.66	9.4
Red beets	11.53	1.04	9.1
Sugar beets	13.50	.88	6.5
Turnips	9.54	.80	8.4
Cucumbers	4.01	.46	11.5
Cabbages	9.48	1.40	14.8
Lettuce	4.13	1.49	19.0
Apples, R.I.G.	17.50	.80	2.1
Strawberries, fruit	9.16	.60	6.5

[1] Many of these are the average results of Jenkins and Winton (Compilation of Analysis of American Feeding-stuffs, Off. Exp. Stas. U. S. Dept. Agl., Bul. 11: 156 pp., 1902).

Knowledge of the ash content is of interest physiologically when related to plant behavior or work.

73. Composition of the ash. — A detailed analysis of the constituents of the ash indicates that through absorption the plant obtains, as a rule, more or less of all of the soluble mineral elements of the soil. Whatever occurs in the soil solution is apt to be found in the plant to at least a slight extent, although the plasmatic membranes of the root-hairs show a certain definite selective absorption, as already indicated. Commonly eleven elements are found in the ash, as follows: phosphorus, potassium, calcium, magnesium, sulfur, iron, sodium, chlorine, silicon, manganese, and aluminium; and, generally speaking, the soil is the only source of these elements. (Nitrogen, likewise derived from the same source, is, of course, a part of the volatile product.)

Chemical analysis cannot determine with any degree of exactness what the plant actually requires from the soil; but it is important because it gives a general indication of the relation of plant to soil solution, it sheds some light upon the general problem of nutrition, and it makes possible an exact computation of the amounts of mineral nutrients which various crops remove from the soil. The table on the opposite page compiled by Kedzie shows the percentage composition of the ash of familiar crops.

From these data it is obvious that there are certain general relations worthy of recollection, such as these: the seed is relatively rich in phosphorus and magnesium, and usually deficient in calcium; stems and leaves may contain much calcium, and often a high per cent of silicon; while the fleshy roots here noted show the highest potas-

COMPOSITION OF 100 PARTS OF THE PURE ASH

	K_2O	Na_2O	CaO	MgO	Fe_2O_3	P_2O_5	SO_3	SiO_2	Cl
Seeds									
Wheat	30.24	.65	3.50	13.21	.60	47.92	—	.73	—
Corn	29.8	1.10	2.17	15.52	.76	45.61	.78	2.10	.91
Flax	26.67	2.22	9.61	15.86	1.11	42.48	—	.88	—
Clover	35.35	.95	6.40	12.90	1.70	37.93	2.40	1.30	1.23
Beans	41.48	1.10	4.99	7.15	.46	38.86	3.40	.65	1.80
Fodders									
Clover	27.25	.80	29.26	8.32	.57	10.66	—	6.18	—
Timothy	34.69	1.83	8.05	3.24	.83	11.80	2.80	32.17	5.20
Corn	27.18	.85	5.70	11.42	.85	9.14	—	40.18	—
Straws									
Flax	34.07	4.37	24.81	15.04	3.67	6.24	—	6.70	—
Buckwheat . . .	46.60	2.20	18.40	3.60	—	11.19	—	5.50	—
Wheat	13.65	1.38	5.76	2.46	.61	4.81	—	67.50	—
Roots									
Potatoes	60.00	2.96	2.64	4.93	1.10	16.86	6.50	2.10	3.40
Sugar-beets . . .	53.10	8.92	6.10	7.86	1.14	12.20	4.20	2.28	4.80
Turnips	45.40	9.84	10.60	3.69	.81	12.71	—	1.80	5.00

sium content. Different parts of the same plant may exhibit great diversity in ash content, indicating an important selective absorption between cells and organs.

74. Effects of conditions upon ash content. — For any particular plant or plant product produced under diverse conditions the ash content is subject to considerable variation; and this variation, while most marked with respect to total ash content, extends also to the ratio of the different elements of which the ash is composed. Official analyses of the sugar-beet show an ash content, calculated to dry-weight, of from 3.2 to 14.6 per cent. There may be a difference with varieties of any plant, but even in the

same variety a marked difference will result when plants grown in Michigan, for example, are compared with those grown on alkali land under irrigation in Colorado. It is to be expected, therefore, that there will occur considerable variation in the ash under different conditions of soil water, fertilization, temperature, and light, or under any conditions affecting transpiration and growth.

75. Ash content at different ages. — It is of interest to note that at different stages of growth the rate of absorption of mineral nutrients and nitrogen bears no constant relation to body weight. Arendt,[1] Bretschneider,[2] and others have shown that in general ash and nitrogen are present in the young plant in relatively greater quantities than in later stages of growth; while starch accumulates relatively more rapidly in the maturing plant. Each of the observers referred to employed oats, and they divided the growing period into five intervals practically as follows: (1) as three to five leaves are unfolded, (2) somewhat previous to full heading, (3) plants in full blossom, (4) beginning of ripening period, and (5) complete maturity. In these experiments the roots were not taken into consideration. The table on the opposite page from Bretschneider shows the absorption of total ash and of nitrogen during different stages. With respect to the absorption of individual constituents, phosphoric acid is obtained in relatively greater quantity during heading, while potash is more rapidly absorbed during the early stages, according to Arendt.

[1] Arendt, "Wachsthumverhältnisse der Haferpflanze." *Jour. f. prakt. Chem.*, **76**: 193, 860.

[2] Bretschneider, "Das Wachsthum der Haferpflanze." Leipzig, 1859.

PERIOD	ASH	NITROGEN
1	8.57	3.59
2, 3	5.96	2.79
4	5.33	2.78
5	5.40	2.43

76. Translocation of mineral substances. — It is well known that as a plant begins to develop fruit or seed there is generally a movement of certain elements or substances to these parts. They may become the storage organs of carbohydrates, proteins, and other organic compounds, but there is also a selective absorption of mineral constituents. Throughout the period of fruit formation phosphoric acid migrates toward the fruiting organs from leaves and stems; and magnesium is invariably translocated, especially from the lower leaves and stem to the younger organs of the upper portion, or to the fruit. Potassium frequently reaches a maximum in the fruiting organs at the time of blossoming, and subsequently may be slightly replaced by

PHOSPHORIC ACID CONTENT AT VARIOUS STAGES OF GROWTH

PART OF PLANT	PERIODS OF GROWTH				
	1	2	3	4	5
Three lower joints, stem	.47	.20	.21	.20	.19
Two middle joints, stem	—	.39	1.14	.46	.18
Upper joint, stem	—	.66	1.73	.31	.36
Three lower leaves	1.05	.70	.69	.51	.35
Two upper leaves	1.75	1.67	1.18	.74	.59
Ear	—	2.36	5.36	10.67	12.52

magnesium. Such substances as lime, silicon, and chlorine do not seem to move appreciably. According to Arendt 1000 oat plants contained in the various periods of growth the quantities of phosphoric acid given in the preceding table, expressed in grams.

77. Water cultures. — From a study of the nutrient requirements of plants in soils, or even in sand cultures, it is not possible to arrive at a definite conclusion respecting the elements needed by plants through the soil solution. For this purpose water cultures are required, and such cultures have been employed for more than half a century in the study of plant nutrition and other physiological relations. Relatively simple experiments afford the chief fundamental facts. Many plants lend themselves to water-culture experiments; in fact all cereals, peas, beans, buckwheat, and many other crop plants may be employed, in spite of the unusual conditions to which the roots are subjected.

The seed represents a considerable accumulation of necessary mineral nutrients as well as organic foodstuffs, and if so supported that the roots may grow in a vessel of distilled water, this supply of nutrients alone may support a strong growth for one or two weeks. If peas or beans are employed and the cotyledons are cut off as soon as the plumule is well developed, the growth in distilled water will be very slight. Ordinary well water, or the seepage water from a tile drain, used as a culture medium, and frequently renewed, affords a vigorous growth.

A water culture containing as soluble salts the elements nitrogen, phosphorus, potassium, calcium, magnesium, sulfur, and iron will afford more or less perfect growth.

Fig. 44. Solution cultures in nutrition work, field peas with and without cotyledons: distilled water (*1*), tap water (*2*), all nutrients (*3*), less nitrogen (*4*), less phosphorus (*5*), less potassium (*6*), less calcium (*7*), less magnesium (*8*), less iron (*9*), and less sulfur (*10*).

These seven elements, in addition to hydrogen, oxygen, and carbon (this last supplied by the carbon dioxid of the air, see Chapter IX), are those indispensable for green plants generally; and the absence of any one of the seven in the nutrient solution will eventually result in the cessation of growth.

In the preparation of the cultures it is convenient to employ as culture vessels ordinary glass tumblers (Fig. 44) covered with black paraffined paper, preferably doubled; a shell of black paper is also fitted over the remainder of the tumbler, and wire guards to assist in supporting the plants as they grow are attached with rubber bands. Canada field peas (*Pisum arvense*) give a quick growth, and are satisfactory for this work. They have the disadvantage of being unusually sensitive to a lack of calcium, as discussed later. Wheat or oats may be used, and these do well, especially when the solution is often renewed. In general, the cereals in solution culture respond quickly at the outset to potassium and to nitrogen, and, relatively speaking, there is often a deficiency of these elements in the seed.

Solution cultures in vessels of the size above noted are important merely for those observations extending over comparatively short periods. Large vessels of the nature of battery jars, permitting the use of several liters of the solutions, are required when it is desirable to bring the plants to an advanced state of growth, or to maturity.

78. Nutrient solutions and water cultures. — The nutrient solution may be variously constituted. It must contain the elements previously mentioned, and it may be well to include also sodium and chlorine. It is probable

that there is no one ideal nutrient solution, since plants vary considerably in their requirements. The solutions given below have been much employed, and they are among those that are generally satisfactory: —

1. Pfeffer's Solution

Calcium nitrate	4 grams
Potassium nitrate	1 gram
Magnesium sulfate	1 gram
Potassium dihydrogen phosphate	1 gram
Potassium chloride	.5 gram
Ferric chloride	trace
Distilled water	3 to 7 liters

2. Crone's Solution

Potassium nitrate	1.00 grams
Iron phosphate	.50 grams
Calcium sulfate	.25 grams
Magnesium sulfate	.25 grams
Distilled water	2.0 liters

The first solution has been more commonly employed. For different plants it is particularly important to change the ratio of calcium to magnesium. This is conveniently done by reducing the amount of calcium nitrate and adding to the potassium nitrate. The Crone solution is reported satisfactory for cereals; but it is more difficult to handle on account of the relatively insoluble iron phosphate.

Water cultures for most seed-plants are preferably slightly acid at the outset, especially where the solution is constituted as in number one. This solution becomes alkaline in time. In the preparation of these solutions for

careful work only the purest distilled water should be employed, and in no case should water from a copper still be considered acceptable for water cultures. Water double distilled from hard glass is preferably employed in accurate work. A method in use at the Bureau of Soils and elsewhere for the treatment of distilled water, such as

FIG. 45. Tobacco in continuous culture: Plat 9, "complete" fertilizer; Plat 10, unfertilized. [Photograph from the Ohio Agl. Exp. Sta.]

might be obtained from a tin-worm still, for instance, consists in shaking up the water with carbon black, or with iron hydrate to free it of any injurious substances.

79. Strength of the nutrient solution. — In the Pfeffer and Crone solutions given above, the concentration is about .1 per cent, or 1 part in 1000 parts of water. This concentration is for many plants sufficiently favorable

in solution cultures. According to Nobbe, nutrient solutions half this strength, on the one hand, or three times as strong, on the other, failed to give the best results with a majority of the plants tested. The higher concentration, however, is far too weak to produce any immediately recognizable osmotic disturbance. The plasmolyzing concentration of KNO_3, for example, would be for many plants 10 to 15 parts per thousand. Nevertheless, from the above facts, it is evident that aside from all financial considerations in the application of fertilizers there is a definite physiological limit to the application of soluble commercial manures.

Neglecting for the moment the effect of the soil upon solubility, an extreme case may be taken: assume that 500 pounds per acre of fertilizer are applied to a loamy soil, and that all of the fertilizer goes into solution. If the water-holding capacity of the soil is 40 per cent and the actual water-content, say, 15 per cent, there would be in the upper 7 inches of soil about 315,000 pounds of water, and the concentration of the KNO_3 alone would be $1\frac{1}{3}$ parts per thousand. This calculation is, of course, far from what would actually occur, for the soil is a strong absorptive matrix, and by no means all of a soluble nutrient added would be effective in the soil solution. Moreover, in most cases, a relatively small quantity of the fertilizers added remains in soluble form.

Commercial fertilizers applied in the drill or in contact with the seed may readily be present in sufficient quantity to be injurious to the germinating seedling. Claudel and Crochetelle[1] find that solutions of 1 to 1000 of ammonium

[1] Annales agron., **22**: 131–142, 1896.

sulfate, sodium nitrate, and some other salts are injurious when applied to seed in pure sand. Newman [1] concluded that on sandy soil 400 pounds of sodium nitrate is unfavorable to the germination of peas. Hicks,[2] reporting upon the germination of seeds as affected by diverse fertilizers, states that, "commercial fertilizers should not be brought into direct contact with germinating seed."

80. The forms of the nutrient compounds. — Since the mineral nutrients (including nitrogen) are available to the plant usually only through the soil solution, it is a general rule that any soluble inorganic salts which are not toxic, or poisonous, may supply the nutrient or nutrients needed. Nitrogen, for instance, in water cultures may be supplied in the form of any of the nitrates. In the field it could not be supplied either as calcium or magnesium nitrate, on account of the greater expensiveness of these compounds. It may be supplied as potassium nitrate, saltpetre; but more extensively as sodium nitrate, or Chilian saltpetre, a common fertilizer. Again, nitrogen is to a certain extent supplied as ammonia compounds, the compound of practical importance being ammonium sulfate. Ammonium compounds are further readily diffused through the soil, and if not used directly, they are, by microörganisms, easily converted into nitrates; hence they may be considered, in general, as readily available forms of this the most expensive of the nutrient elements. In this connection it is important to note that it is only after decompo-

[1] Arkansas Agl. Exp. Sta., Bul. **34**: 99–124.

[2] Hicks, G. H., "The Germination of Seed as Affected by Certain Chemical Fertilizers." Div. Bot. U. S. Dept. Agl., Bul. **24**: 15 pp., 2 *pls.*, 1900.

sition and conversion into ammonia and nitrates that the numerous important organic nitrogen fertilizers, such as stable and green manures, dried blood, tankage, and the like, are to any practical extent valuable for plants. Decomposition and nitrification processes, however, will be discussed later.

FIG. 46. Tobacco experiments: Plat 1, no fertilizer; Plat 2, acid phosphate. [Photograph from the Ohio Agl. Exp. Sta.]

The soluble phosphates of the various bases are all immediately available and may be used in water cultures; but phosphates are frequently applied to the soil in some insoluble form, such as bone-meal or phosphatic rock, which become gradually available by chemical changes in

the soil, and by root action. The common phosphatic fertilizers are the four phosphates of lime, and the only one of these which is soluble is the saturated, or superphosphate $[Ca(H_2PO_4)_2 + H_2O]$, although the reverted or dicalcic phosphate is also readily available.

Many soluble forms of potash might be used, but the important commercial forms are the sulfate, chloride (muriate), and carbonate. In quantity the chloride is injurious to some crops. The chief sources besides ashes are now the crude products of the German potassic mines.

81. Plant nutrients in rock. — It is more particularly the province of instruction in soils and economic geology to consider the origin of the plant nutrients of the soil. The geological history is, of course, of no physiological significance; it is information; so that it is here sufficient, by way of reference, to note some few of the more important facts.

The rocks of the earth's crust from the oldest to the most recent, from the hardest to the softest, whatever may have been their origin, are made up of a variety of minerals, some of the chemical constituents of which are the elements previously noted as necessary in the growth of plants. Even the hardest granites, basalts, and lavas contain, in general, a small percentage of potash, soda, lime, magnesia, and iron. A single form of rock, such as one of the red granites, may be deficient in magnesia; another, like a red, soil-forming basalt, may lack in potash; whilst a limestone may contain no iron. The plant nutrients form commonly a minor portion of the bulk of the rock, the balance consisting often of silica and alumina.

The following table shows the distribution of the substances mentioned in a few types of rocks:[1] —

	Granitic	Basaltic	Lava (Vesuvius)	Limestone (Virginia)	Limestone (Dolomitic)
Silica (SiO_2)	69.80	53.13	48.12	4.13	
Alumina (Al_2O_3)	14.45	13.74	17.16	4.19	
Ferric oxid (Fe_2O_3)	2.62	1.08	10.82	4.33	
Ferrous oxid (FeO)	1.94	9.10		2.35	
Lime (CaO)	1.84	9.47	9.84	44.79	53.4
Magnesia (MgO)	.49	8.58	3.99	.30	44.2
Soda (Na_2O)	3.91	2.30	2.77	.35	
Potash (K_2O)	3.96	1.03	7.24	.16	
Phosphoric acid (P_2O_5)	.10	.40	—	3.04	
Carbonic acid (CO_2)	—	—	—	34.10	
Ignition and loss	.89	1.17	—		

Practically, no soil is made up of mineral constituents in the same proportion as they occur in the original rock. There are losses and gains of plant nutrients with respect to any one type of rock, but residual soils, referable to the decomposition of a particular rock, approach the rock more nearly. In general, however, it is clear that, since soils are formed by the grinding down and decomposition of rocks, they may contain all the minerals of the earth's crust. A soil is ordinarily of complex origin, and aside from this, the chief qualities which make it a favorable environment for the plant as contrasted with broken rock

[1] For a comprehensive treatment of the composition of original rock and residual soils derived therefrom the student should consult the following: Lyon and Fippin, "Soils," pp. 1–68; Bailey, "Cyclopedia of American Agriculture," I (Chapter X): pp. 323–371.

or coarse sand may be chiefly three: (1) comminution and greater water-holding capacity, previously discussed; (2) the addition of accumulated organic matter, and (3) the presence of a variety of microörganisms, gradually transforming the organic matter. The fine state of division of the soil particles also permits great freedom to the further weathering influences of water and other factors concerned in the rock disintegration which is constantly in progress.

82. Soil fertility. — Fertile soils will generally contain an abundance of the soil nutrients, sufficient to produce crops for many successive years. This does not necessarily imply that the nutrients are available in proper ratio. Intelligent growers, moreover, consider not merely the present production of crops, but also the maintenance of high fertility in the case of fertile soils, and the development of fertility in unproductive soils. It is necessary, then, to have in mind the supply and the source of supply of the important elements and their relative abundance.

Sulfur and iron may be dismissed from further consideration, since they are naturally abundant in soils, and are used by plants in such limited quantities that a dearth of these nutrients is not common. As would be expected these two elements are only incidentally constituents of commercial fertilizers. Magnesium is also ordinarily present in sufficient quantities, and it may be present in such excess as to be harmful, as noted later. The plant producer is now certain that more attention must be paid to lime, and especially to the relative abundance of lime and magnesia. Furthermore, when liming is required every few years, it is a good custom to determine for any

soil the value of using, about once in twelve or fifteen years, a lime with high magnesia content. Finally, of all the important elements furnished by the soil, nitrogen, phosphorus, and potassium are less abundant, relatively more in demand by the growing crop, and accordingly to be conserved and consistently restored.

83. Nutrients removed by farm crops. — In order to appreciate properly the relation of cropping to the fertility of the land it is necessary first to note the amounts of the more important soil nutrients — nitrogen, phosphorus, and potassium — which may be removed by various crops annually. The table below is adapted from data given by Hopkins:[1] —

Crops	Yield	Amount in Pounds removed per A.			Value of Nutrients per A.
		Nitrogen	Phosphoric Acid	Potash	
Alfalfa hay	5 tons	250.0	22.5	120.0	47.40
Clover hay	3 tons	120.0	15.0	90.0	25.20
Timothy hay	2 tons	48.0	6.0	47.7	10.76
Potatoes, tubers	200 bu.	42.0	8.7	60.0	10.94
Sugar-beets, roots only	15 tons	80.0	14.4	125.6	21.26
Corn, grain	60 bu.	60.0	10.2	11.4	
Corn, stover	1.8 tons	28.8	3.6	31.2	
Corn crop	——	88.8	13.8	42.6	17.52
Wheat, grain	30 bu.	42.6	7.2	7.8	
Wheat, straw	1.5 tons	15.0	2.4	21.0	
Wheat crop	——	57.6	9.6	28.8	11.52
Apples	400 bu.	31.3	3.3	38.0	7.38

[1] Hopkins, C. G., "The Fertility in Illinois Soils." Ill. Agl. Exp., Bul. 123: p. 189.

In the preceding table it is shown significantly that the amount of nitrogen taken up by the leguminous crops reaches a figure averaging far above that of the others. As indicated later, much of this nitrogen is derived from

FIG. 47. Fertilizer experiments with cereals and grass; to the right, effect of a nitrate.

the air through the remarkable activity of the bacteria of the root tubercles; and in reality it often represents, even with the harvesting of the crop, a soil gain. It would represent a large soil gain if the crop were returned to the

land. In general, for the crops included, the losses of nitrogen and potash are fairly comparable, while the loss of phosphorus is only about one fourth as great as either of the other constituents. Frequently, however, much of the potash-containing products, such as straw and stover, are returned to the land.

84. Nutrients removed by fruit crops. — The following table indicates the amounts of nitrogen, phosphoric acid, potash, and lime removed by various fruits, the quantities being determined for the fresh fruit per thousand pounds, assuming that leaves, wood, etc., of the trees will be eventually returned to the soil: —

Quantities of Soil Ingredients withdrawn by Various Fruits[1]

Fresh Fruit 1000 Pounds	Amounts of Nutrients Removed, in Pounds				
	Total Ash	Nitrogen	Phosphoric Acid	Potash	Lime
Almonds[2]	17.29	7.01	2.04	9.95	1.04
Apples	2.64	1.05	.33	1.40	.11
Apricots	5.08	1.94	.66	3.01	.16
Bananas	10.78	.97	.17	6.80	.10
Cherries	4.82	2.29	.72	2.77	.20
Chestnuts[2]	9.52	6.40	1.58	3.67	1.20
Figs	7.81	2.38	.86	4.69	.85
Grapes	5.00	1.26	.11	2.55	.25
Olives	13.50	5.60	1.25	9.11	2.43
Oranges	4.32	1.83	.53	2.11	.97
Prunes, French	4.86	1.82	.68	3.10	.22
Walnuts[2]	12.98	5.41	1.47	8.18	1.55

[1] Data taken from Wickson, E. J., "California Fruits," p. 157, 1900.

[2] Including hulls.

It is also further interesting to note the requirements per tree and also per acre in the case of certain fruits, as shown in the following tables reported by the New York Experiment Station: —

IMPORTANT NUTRIENTS USED DURING A GROWING SEASON BY MATURE FRUIT TREES[1]

Fruit	Amount Removed per Tree, in Pounds				
	Nitrogen	Phosphoric Acid	Potash	Lime	Magnesia
Apple	1.47	.39	1.57	1.62	.66
Peach	.62	.15	.60	.95	.29
Pear	.25	.06	.27	.32	.09
Plum	.25	.07	.32	.34	.11
Quince	.19	.06	.24	.27	.08

NUTRIENTS USED PER ACRE BY DIFFERENT FRUIT TREES[2]

Variety	No. Trees per A.	Amount removed per A., in Pounds				
		Nitrogen	Phosphoric Acid	Potash	Lime	Magnesia
Apple	35	51.5	14.0	55	57.0	23
Peach	120	74.5	18.0	72	114.0	35
Pear	120	29.5	7.0	33	38.0	11
Plum	120	29.5	8.5	38	41.0	13
Quince	240	45.5	15.5	57	65.5	19

[1] N. Y. Agl. Exp. Sta., Bul. 265: p. 366.
[2] *Ibid.*, p. 369.

AMOUNTS OF NUTRIENTS REMOVED PER ACRE BY THE FRUIT[1] ALONE

PART OF TREE	VARIETY OF FRUIT TREE	NITROGEN	PHOSPHORIC ACID (P_2O_5)	POTASH (K_2O)	LIME (CaO)	MAGNESIA (MgO)
		Pounds	Pounds	Pounds	Pounds	Pounds
Fruit . . .	Apple	20.0	8.5	45.0	3.9	6.4
Fruit . . .	Peach	17.5	8.6	36.0	2.2	4.1
Fruit . . .	Pear	9.0	3.2	20.2	2.2	2.6
Fruit . . .	Plum	13.3	4.7	18.5	4.4	3.0
Fruit . . .	Quince	20.0	10.0	44.4	3.4	6.0

Assuming that the leaves, dead twigs, etc., are annually returned to the soil, fruits are ordinarily less exhausting than field crops. In this connection it is entirely immaterial that a bushel of oats of the same variety, or a barrel of Baldwins, will not always contain the same amounts of nitrogen, phosphoric acid, and potash. Other analyses, therefore, will not accord in detail with those given. The fact that these crops are not exhausting is important in contemplating the maintenance of fertility in intensive fruit production. It would seem that in fruit production it may easily be possible to realize a permanent system of agriculture.

85. Amount of nutrients in soils. — Fertility is a matter so complex — dependent upon such a variety of factors — that a chemical analysis is important in two respects, chiefly: (1) to indicate the total amounts of plant food, for the time available or unavailable, and (2) to point out unbalanced conditions, or to suggest lines of treatment. Ultimately, experiments with the plant are invariably

[1] *Ibid.*, p. 370.

required in order to determine what is, for any soil, the most effective fertility.

Many analyses of tillable soils have been made throughout the United States, and it is shown that the storage of nutrient elements therein is most diverse. Calculated to pounds per acre in the upper seven inches of soil many complete analyses afford extremes as shown in the following tabular summary: —

Nutrient	Amount per A.
	Pounds
Phosphoric acid	500 to 10,000
Potash	3000 to 100,000
Lime	2000 to 200,000
Magnesia	1500 to 150,000

When the distribution of the roots and the availability or lack of availability of the compounds are taken into consideration, it is evident that with respect to the minima one may speak of exhaustion or lack of nutrients, but with respect to the maxima there may be sufficient, conservatively used, for generations.

A very thorough study is being made of the soils of Illinois, and the table on the opposite page gives the average amount of plant food for a variety of soil types.

These represent, except in the last two cases, the total plant food in 2,000,000 pounds of dry surface soil, this weight being approximately that of 7 inches of ordinary soil. In the case of sand, which is heavier, about 2,500,000 pounds are concerned in the same depth, and in the case of the light peat only about 1,000,000 pounds.

Soil Type	Total Nitrogen	Total Phosphorus	Total Potassium
Gray silt loam	2,880	840	24,940
Brown silt loam	5,035	1230	35,792
Black clay loam	7,228	1755	33,510
Yellow silt loam	2,016	884	33,901
Brown sandy loam	3,070	850	26,700
Brown bottom loam	4,720	1620	39,970
Sandy soil	1,440	820	30,880
Deep peat	34,880	1960	2,930

The vast array of facts which have been developed with respect to the amount of nutrients in soils is, after all, of somewhat limited application. This is due in large part to fundamental difficulties in obtaining a satisfactory basis for a computation of effectiveness. If, for example, the total quantities of the nutrients contained in the first few inches of soil are made a basis, then, to modify the calculations of the amounts of the nutrients, there are such conflicting factors as the following: —

(1) Roots are not commonly limited to the first 7 or 10 inches of soil (Fig. 9).

(2) To a certain extent there is in the soil a movement of the soluble nutrients from higher to lower levels and also the reverse. There is further a variable loss from leaching.

(3) The roots do not actually come in contact with all of the soil, and the special solvent action (discussed later) is greatest in the immediate vicinity of these structures.

(4) No absorbing organs are able completely to "exhaust" or remove all the nutrients from any soil, and the amounts readily removable depend upon complex chemical and physical factors.

86. Availability of the nutrients. — Plant nutrients exist in the soil in conditions most diverse with respect to availability, and chemical analysis does not satisfactorily distinguish between availability and nonavailability. Potassium, for example, may be present in conjunction with aluminium silicate, or it may be present in far more soluble form; but there are at present very few data concerning the nature of these compounds. If any element is present in markedly unavailable form, that element will be needed as a fertilizer, especially to hasten the early stages of growth.

Fertilizers are generally applied, not only to keep up fertility, but to increase availability. In the latter case, therefore, from the immediate standpoint of the plant, fertilizers are supplied either (1) as directly available nutrients; (2) as substances, effecting readjustments in the soil, so that needed elements become more available to the plant; or (3) in order to counteract the effects due to some unbalanced condition of the nutrients (later discussed at length), injurious acidity, alkalinity, and the like.

87. The solvent action of roots. — It is well known that roots and root-hairs are able to render available a certain amount of nutrient materials. There is a solvent action of the roots. The case almost universally cited is the corrosion of marble (limestone) by roots. The nature of this solvent action has been much studied and discussed. It is certain that the excretion of aqueous CO_2 is sufficient to account for much, and probably for nearly all of this action.

Kunze and others seem to have convincingly demon-

strated that there is no excretion of a mineral acid, and that any organic acids present are beyond the sensitiveness of litmus. Nevertheless, some investigators have found other acids present under certain conditions. These conditions are mainly poor oxygen supply. Stoklasa and Ernst, for example, have identified traces of acetic acid and formic acid with poor oxygenation of the roots of corn and barley. Under such circumstances these may be regarded as evidence of unfavorable surroundings, and not as excretions beneficial to the plant. Under similar circumstances oxalic acid was identified in the case of the sugar-beet and of the hyacinth. From the preceding it seems safe to assume that in the case of cultivated plants normal solvent action is due to CO_2 (an excrete product produced by every living cell; cf. respiration).

It should be observed, however, that recent studies by Schreiner and Reed call special attention to the oxidizing action of roots. This seems to be brought about by a peroxidase, and the process may be practically important, since many cultural practices are designed to promote oxidation.

88. CO_2 excretion and the availability of phosphorus. — Stoklasa and Ernst have further given some data indicating that the relative rate of excretion of CO_2 by the roots per gram of dry weight of substance is directly important in determining the capacity of a plant to get phosphoric acid from the more insoluble substrata. The following table exhibits side by side the excretion of CO_2, as shown by water cultures, and the absorption of phosphoric acid when the same kinds of plants are grown in gneiss and basalt: —

Plants grown 90 Days at 20° C.		Plants grown 77 Days	
	CO_2 excreted per 1 gr. Substance. Mg. per 24 hr.	Substratum	P_2O_5, Per Cent in Dry Substance
Barley	74.6	Gneiss	.285
		Basalt	.297
Wheat	89.6	Gneiss	.363
		Basalt	.443
Rye	110.8	Gneiss	.368
		Basalt	.465
Oats	118.9	Gneiss	.534
		Basalt	.631

89. **Another view of soil fertility.** — In the discussion of fertility thus far it is accepted that soils may be relatively deficient in nutrients, that removal of nutrients by crops tends towards practical deficiency, and that the addition of fertilizers, although it may also affect availability, or balance, is a considerable factor in maintaining fertility. Some investigators advocate another view. This is in part based upon a method of observation and experiment yielding results which seem to point to an unexpected uniformity in the constitution of the soil solution from diverse types of soil.

They conceive that the addition per acre of a few hundred pounds of fertilizers to one or two million pounds of earth (surface soil) is of no consequence in increasing available nutrients, and they would ascribe the admitted value of fertilizers to some more general effects upon the soil, all of which are not understood. This view would seem to demand that sodium chlorid would be, in general,

as valuable a fertilizer as potassium chlorid or sulfate. We must regard as one of many types of facts opposed to this view the vast amount of experimental work showing the direct value of particular nutrients, and more especially, of particular nutrients at certain stages of the growth of the crop. The view is of undoubted value in suggesting lines of investigations. Associated with it, usually, is the idea of toxic excreta from plant roots, which is considered in another place.

90. The paraffined wire basket in nutrition studies. — In determining through plant growth certain soil relations by a quick laboratory method it has been the custom to employ tumblers or other similar glazed vessels from which there could be no loss of the materials employed. These are not always satisfactory, since, if drying out proceeds, spaces are left between the soil and the vessels, and under unfavorable conditions, especially, it is in these spaces that the roots grow, thus giving no exact indication of the soil conditions.

The paraffined basket method is well demonstrated by Figure 48, in which, from left to right, successive stages in the preparation of the culture are shown. As described by Schreiner, the basket is dipped top downward into hot paraffin several times until a rim is made. It is then filled with soil to the rim, and firmly packed near the gauze, the surplus protruding soil being brushed off. The basket is then dipped into the paraffin up to the rim several times. The paraffin penetrates into the soil pores or capillaries, and there is no line of cleavage, as with glazed vessels. The surface of the soil may be covered with paraffined paper, in which slits are made for placing the seedlings.

The method has been much used in connection with Livingston's plan of using transpiration as a measure of

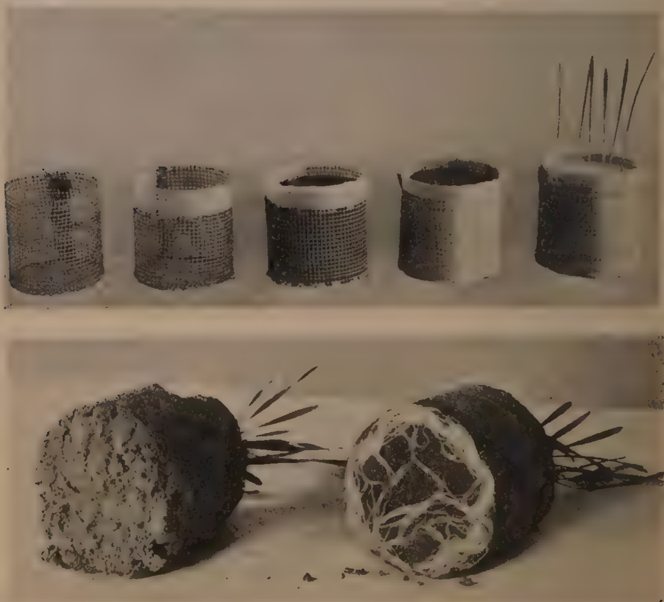

Fig. 48. The paraffin-basket method. Upper illustration shows sequence of stages in preparing cultures, and the lower a comparison of root growth in a basket (left) with a tumbler (right). [Photograph from the Bureau of Soils, U. S. Dept. Agl.]

growth, but it has a much wider application, whatever the indicator may be, in the general study of the mineral nutrients of the soil, and many other soil conditions. This method is unnecessary where the conditions of soil moisture are constant, and with grades of coarse sand.

Again, such plants as corn and vigorous varieties of the sunflower are able to force the roots through the paraffin, especially in warm weather.

LABORATORY WORK. — SUGGESTED EXPERIMENTS

Solution cultures, essential nutrients. — Since the seed represents a considerable accumulation of the necessary food-materials required by the growing plant, the absolute necessity of a particular nutrient may not be readily demonstrated except by growing plants to maturity in relatively large vessels. The latter is commonly impracticable, and in simple experiments it suffices to determine the comparative effects upon growth or green weight of a full nutrient solution, along with other solutions lacking each element in turn. While the method is open to criticism, the student will find much use for the experience in manipulation; and after a study of balanced solutions, he may define his criticism.

Materials needed: cheap tumblers covered and arranged as suggested (section 77 and figure 44), or wide-mouth bottles with flat corks notched to receive the seed; black paper shells for darkening the cultures, and black paper circles or squares dipped in hot paraffin for tumbler covers; chemicals required by the solution; as many stock flasks, or bottles, as nutrients; distilled water, graduates, rubber bands and labels; and germinating seed.

Uniform seedlings should be employed, and these should be grown on moist moss or sawdust, or upon a paraffined wire screen floated on water by corks, but sufficiently weighted to keep the seed moist. All vessels should be chemically clean (preferably by the acid-dichromate method), and only the purest chemicals and distilled water employed.

Prepare a stock solution of each main constituent of the Pfeffer solution in the proportional quantity of water, thus for a 5000 cc. solution, as follows: —

Calcium nitrate, 4 grams in distilled water 1000 cc.
Potassium nitrate, 1 gram in distilled water 1000 cc.
Magnesium nitrate, 1 gram in distilled water 1000 cc.
Potassium dihydrogen phosphate, 1 gram in distilled water 1000 cc.
Potassium chlorid, .5 gram in distilled water 1000 cc.

Taking 50 cc. of each of the preceding, cultures of the full nutrient solution lacking iron are prepared, the iron being added in every culture where desired by a few drops of a 2 per cent solution of the salt indicated.

In omitting the several elements separately, substitutions are made from solutions of other salts made up in the same proportion, but taking cognizance, in each case, of the smaller quantity desired, the following substitutions being recommended: —

Less calcium,	use $NaNO_3$.
Less nitrogen,	use $CaCl_2$ and KCl, respectively.
Less potassium,	use $NaNO_3$, NH_2PO_4, and NaCl, respectively.
Less phosphorus,	use KCl.
Less magnesium,	use Na_2SO_4.
Less sulfur,	use $MgCl_2$.

Set up duplicate cultures with full nutrient solution, with solutions lacking each element successively, with distilled water, with tap water, with Crone's solution. Also make for comparison cultures of the Pfeffer solution both five times the strength and one fifth the strength of that above used. Also set up two additional tumblers (employing the full nutrient solution) of peas to be employed in the last experiment.

If it is possible to include tests with several plants, Canada field peas, oats or wheat, and buckwheat are important, for each manifests special requirements in the early stages of growth depending largely upon the composition of the seed.

Use ten plants in each culture, keep in a fairly moist place (or invert a tumbler over each culture) for a day or two, then transfer to greenhouse, if possible. Replace, as needed, by pipette

the water lost by transpiration. If the cultures are continued longer than two weeks, renew the solutions. When necessary, support the plants by the wire standard and ring (Fig. 44). Close the experiment within four weeks, measuring tops, weighing roots and tops separately, taking notes on general appearance, tabulating results, and representing graphically the green weight of tops and of the whole plant.

Corrosion by roots. — Place the polished marble plates provided in the small germinating plats (cigar boxes 2 inches deep answering well), cover with 2 inches of sand, sow seed of squash and bean, and maintain under conditions favorable for growth. When the seedlings have grown vigorously to a height of 5 or 6 inches, examine the marble plates for etched tracings.

Determination of acid excretion by roots. — When the two additional tumblers employed in a preceding experiment with nutrient solution afford vigorous seedlings, set up the following experiment: Boil one liter of tap water in a flask, cool, and aërate, make slightly alkaline with potassium hydrate, and add a few drops of phenolphthalein to give distinct pink color. With this solution fill four tumblers, two of which are to be covered with paraffined paper as controls; to the other two transfer the covers and seedling peas above indicated. Place both sets under similar conditions, and after 24 hours note and compare the color in the two cases. If the pink color has disappeared, the solution has become acid. In that case pour the contents of one tumbler into an evaporating dish, and bring to a boil. If the color reappears promptly, it indicates carbonic acid.

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CHAPTER VIII

SPECIAL FUNCTIONS AND RELATIONS OF MINERAL NUTRIENTS

THE RÔLES OF MINERAL NUTRIENTS

Plant physiological literature contains many references to the specific rôles or effects of the various mineral nutrients. Some of the observations and results are of particular interest; but many of the suggestions are based upon such slight evidence as to require no consideration in this place. It is an interesting and important field of work, but explanations of many of the effects which have been noted are more easily formulated than proved, and a satisfactory interpretation of the results is proving most difficult.

The method of inquiry involves, on the one hand, a study of the effects produced upon the plant or cell when an element is, as far as possible, eliminated; or, on the other hand, observations upon the results of supplying the particular nutrient element under study when it has been deficient. These are practically the only methods which can be employed; but it must be admitted that the absence of any nutrient may lead to unbalanced conditions which may induce general pathological effects, so that the particular primary rôle may be obscured. An analogous

criticism would be equally valid in many other lines of investigation.

91. The nature of the special rôles. — Certain soil elements are needed in the building up of the permanent proteins of the living matter. Those which are known to enter invariably into the composition of albuminoidal or protein bodies are necessarily of first importance. Other essential mineral elements play only doubtful rôles in protein activities, yet they have evidently such important functions to perform in connection with the activities of the protoplasm and its products as to be indispensable.

Practically, as expressed by Reed, we may say that in general essential elements appear to function in two ways: (*a*) as component parts of necessary cell structures and fluids; and (*b*) as agents indirectly essential, by causing less understood physical or chemical reactions, — acting as carriers of other ions, as specific antidoting agents, or otherwise.

The first group includes, among the elements now under discussion, nitrogen, phosphorus, and sulfur; while potassium, calcium, magnesium, and iron fall apparently in the second group. If the chemical work of the future demonstrates fully the existence of the basic proteins, now postulated, as noted later, it would then only, perhaps, be safe to assume the incorporation of these elements into the protoplasm itself. The latter elements (especially potassium) may be important in the osmotic work of the cell, requisite as carriers or accumulators of food atoms, as catalytic agents, etc.; but with nitrogenous bodies like proteins they seem to form at most only temporary combinations.

92. The rôle of phosphorus. — Phosphorus is indispensable primarily because it is a necessary constituent of the nucleo-proteins of every living cell. It is accumulated in relatively large amount in the seed, so in the younger stages of growth, when practically all cells are embryonic, it is relatively most abundant.

Many observers have commented upon the prompt migration of the sum total of phosphorus compounds from maturing stems and other older vegetative parts to the growing tips or to the developing seeds. It has been shown by Wilfarth and his associates that during the ten days from June 17 to 27, as barley is maturing, there is a striking change in the phosphorus relations, the amount in the straw being reduced from 29.04 kilograms to 9.59; while in the grain there is an increase in the same time from 3.54 to 29.84 K. per hectare. At the same time they give data which they interpret to mean the movement of some phosphorus back into the soil.

Loew was the first to suggest important additional functions of phosphorus. As a result of phosphorus hunger the cells of Spirogyra soon cease to grow, but starch is formed for a time. He also found that oily and protein substances were not used, but in fact accumulated in the cell. Owing to the phosphorus content of lecithin, he explained the accumulation of fats by assuming that such substances are changed into lecithin before becoming assimilable by the protoplasm; thus phosphorus would be essential in the assimilation of fats.

Overton assumes that lecithin and similar bodies are important in the osmotic properties of the plasma membrane, this view being largely based upon the penetrability

of the membrane to substances like alcohol. There are, however, serious objections to this idea. Reed found, among other pathological conditions attending an insufficiency of phosphorus, that starch was transformed into unusual carbohydrate forms, and that cell-walls were often thickened.

93. The rôle of potassium. — Potassium is an essential element, and the experiments which have been carefully and accurately carried out make it possible to say that in general there may be no fairly complete substitution of potassium by means of the related metals, lithium, sodium, rubidium, and cæsium, and generally very slight partial substitution among higher plants. It is, however, true that, when potassium in sufficient quantity is not available, the addition of sodium is almost invariably attended by increased growth. The relation to sodium is discussed more at length later.

Potassium in organic food formation. — Many investigators agree in assigning to potassium a peculiarly important function in the formation of carbohydrates and proteins. Loew and Reed have devoted special attention to this point. When potassium fails, starch is not formed, and even if sugar is furnished, proteins are not normally produced. Cells in a condition to divide are also considerably influenced by lack of potassium. Such cells might elongate to twice their normal length, supposedly by a process of stretching, but there would be no evidences of cell or nuclear division. Loew regards the potassium as a strong condensing agent (and he shows that in certain cases potassium is able to effect changes which sodium will not). Since condensation processes are probably

involved in carbohydrate, fat, and protein making, the relation of potassium to general metabolism is deduced.

The potassium and protein relation. — The relation between protein and potash in storage organs has also been shown to be suggestive, at least to this extent: Seeds or other organs rich in protein are generally relatively rich in potash, although there is no definite ratio. Loew cites certain analyses of Wolff which may be summarized in the following table: —

Product	No. Species	No. Analyses	Potash, Per Cent in Ash	Protein, Per Cent	Potash Avg. Per Cent	Protein, Avg. Per Cent
Seeds of cereals	5	200	16.32 to 31.47	9.8 to 11.0	23.07	10.2
Seeds of legumes	6	64	29.84 to 44.01	22.7 to 35.3	39.21	29.0

The osmotic relation and winter injury. — It has been generally held that another important rôle of potassium may be found in its action as an osmotic agent. Some plants contain relatively large quantities of potash in their juices, as K_2SO_4, KNO_3, KH_2PO_4, and certain organic salts. Other plants, however, have high osmotic coefficients on account of organic substances, and there seems to be no sufficient reason why as an osmotic agent the potassium is to be regarded as having a constant rôle. In fact, the view seems to be justified that in so far as potassium is necessary osmotically it may be replaced by sodium. Certainly the high osmotic value of certain fungi which may grow upon strong sugar or nutrient solu-

tions is not due to the presence of K compounds, and this fact has been abundantly demonstrated.

With this osmotic relation in view, it was natural that there should exist also the belief that plants afforded an abundance of potash are better able to withstand drought. This is not yet sufficiently proven. Resistance to drought may possibly be due in part merely to increased salt content of the plant; in which case, however, it would be inferred that many soluble salts should have a similar effect. The latter is not reported to be the case. The experiments of Atkinson in Alabama on the prevention of "rust" of cotton have been interpreted to mean that potassic fertilizers are partially important in the water relation of the plant, guaranteeing sufficient water, consequently preventing the blight, which is a combination of drought and fungous effects. Nevertheless, there is apparently no evidence that desert plants possess any particular relation to potassium. It is also claimed that by virtue of relations to the water-content plants well supplied with potash would be less injured by freezing.

Maturity, quality, and color. — The belief is current that orchard trees well fertilized with potash ripen their wood more thoroughly, and that as a partial but direct consequence of this the shoots and buds are not so subject to winter or early spring injury. In other words, the belief indicates that potash content is a special factor in the hardiness of perennials. Heightened color and quality in apples has also been attributed to it, but a careful examination of this point indicates that there is no such relation. It seems rather that such a deficiency of any element as to check growth necessarily affects quality.

94. The rôle of magnesium. — Magnesium is an element concerning some of the functions of which practically all physiologists seem to be agreed. It may be inferred that it does not play a direct rôle in the formation of proteins. It is, in general, more toxic to protoplasm than the other mineral nutrients, and according to Loew its chief function is probably to be found in the conveyance of phosphoric acid for assimilation. Magnesium is more abundant in those parts of the plant undergoing development, as in growing tips and seeds. This would imply that it acts indirectly to condition the formation of the nucleo-proteins. Loew believes that "the same amount of base can serve over and over again as the vehicle for assimilation of phosphoric acid." It is well known that magnesium is migratory in the plant, so that maturing organs are considerably depleted. Attention has been called to the fact that oily seeds contain a larger proportion of this element than do starchy seeds, and this is regarded as a point strengthening the argument of Loew respecting the function of this element, especially since lecithin is formed in cells rich in oil. Reed has also found that there is some definite connection between magnesium and phosphorus. He has demonstrated that oil globules are not formed in Vaucheria when magnesium is lacking in the nutrient solution, and he believes that there is an intimate relationship between magnesium and vegetable oils.

95. The rôle of calcium. — The judicious use of lime in plant production may be the determining factor in the active fertility of a soil. It appears that the addition of lime to soils is a practice which has shown more or less alternation in various agricultural epochs. Wheeler

has suggested a cause of this use and disuse. When the benefits from it at any time became known, this probably led to excessive use, causing injury, whereby the practice again fell into disfavor. In the United States a careful study of the liming practice and of its effects has been made in comparatively recent years.

Calcium has functions to perform which are strictly physiological; that is, directly important in the metabolism of the plant; it has other effects distinctly ecological, affecting the plant through its action upon the physical and chemical environment. It is not always possible to distinguish the one form of effect from the other. From an agricultural standpoint Wheeler has given in the "Cyclopedia of American Agriculture" a concise enumeration of the effects. In this connection the physiological side requires more particular consideration.

In vegetative organs. — There is generally a considerable accumulation of lime in leaves and other vegetative organs, and on this account it has been assumed to play an important rôle in some of the functions associated with the chlorophyll. Up to a certain point calcium hunger does not affect starch formation, and the evidence points rather to an inhibition of starch and other carbohydrate digestion and transport. In fact, many fundamental experiments have established a definite relation — whether direct or indirect it is impossible to say — between calcium content and starch digestion. The addition of soluble carbohydrates is generally beneficial where plants lack calcium. In this connection it is of interest to note that calcium is apparently not required by fungi and some of the lower algæ, yet it is required by higher plants forming no starch.

Other investigators regard calcium as important, in the main, in the neutralization of oxalic acid and acid oxalates, assumed to be a factor in protein synthesis. Neutralization is often effected in this way, for calcium oxalate is of frequent occurrence; yet in some of the higher plants there is no such accumulation of oxalates.

Boehm considered calcium essential in the formation of the cell-wall, and while he erroneously interpreted this to be similar to the use of calcium in bone formation, yet the relation of an adequate calcium supply to the formation of cell-walls has been clearly brought out by many investigators. This apparent function may be merely an indication of imperfect use of carbohydrates as above discussed. Moreover, the formation of complete cell-walls in the various fungi without calcium is against any supposition of its direct importance in modified cellulose formation.

As early as 1880 it was ascertained that salts of magnesium are toxic when used alone, and that this toxicity disappears when sufficient calcium is present in the nutrient solution. In recent times the peculiar and antagonistic relation which exists between calcium and magnesium, and also between other nutrient elements to a less extent, has been more completely developed. The work begun by Von Raumer, and followed up by Loew, Loeb, Kearney, and Osterhout, will be discussed at greater length under Balanced Solutions. It is necessary, at this time, merely to indicate that calcium is important in preventing the injurious effects of an excess of magnesium.

Calcium in protein formation. — In studying this relation of the elements, Loew has developed an important

N

hypothesis respecting the rôle of calcium in protein formation. According to him we must anticipate a calcium-protein compound as important in the building up of the nucleus and plastids of the cell. In the absence of sufficient calcium he believes that magnesium takes its place, and that this magnesium compound does not possess the necessary capacity for imbibition phenomena required by the cell structures. There are some important objections to be met in considering this hypothesis, in view of the

Fig. 49. Effect of liming in the production of alfalfa; no fertilizer (*1*), lime only (*2*), and lime with nitrogen (*3*). [Photograph from the Rhode Island Exp. Sta.]

facts that magnesium salts are not toxic for the fungi and for the lower algæ, and, in the presence of small amounts of calcium, relatively nontoxic also for the marine algæ, as well as for a few of the higher plants.

On the other hand it is true that plants grown in solutions lacking calcium show, coincident with the expected pathological conditions, an increase in the magnesium content, whereas other pathological effects produced by unfavorable conditions show a normal ratio of calcium and magnesium.

Chemical effects. — Lime is almost as important through its action in rendering the soil environment chemically favorable as in its specific rôles in cell metabolism. Soils in which vegetation is growing have, in general, a tendency to develop the condition fittingly termed acidity. When the acidity increases beyond a certain point, it may become extremely inhibitory to the proper growth of a variety of agricultural plants, and lime, either as carbonate or as slaked lime, is necessary in order to neutralize this condition. The carbonate of lime is less injurious and more generally applicable in large quantities.

The ecological relation of plants to soils containing much or little lime is particularly interesting, and has been extensively studied from the standpoint of the adaptability of crops and of the distribution of wild plants as well. Upon the crop side Wheeler has contributed excellent data. In general, the experiments indicate that when the soils show a marked acid tendency, liming is beneficial.

Some of the plants to which the greatest benefit accrues are such as lettuce, beet, onion, and cantaloup. Again, crops such as cranberry, watermelon, red-top, cow-pea, and others may be favorably influenced when the acidity is considerable. The great majority of crops occupy an intermediate position, many responding satisfactorily under field conditions to moderate liming. Upon some Rhode Island soils the yield of sugar-beets has been increased by liming up to one hundred fold. Liming will also affect, within the season, the character of the weeds or native vegetation. It is of interest to note that closely related plants are differently affected; thus the watermelon and the muskmelon, or red-top and timothy, may be

contrasted, the last-named in each case enduring much less acidity.

Lime is important in effecting a liberation of (by rendering available) other nutrients, and on this account it should be used cautiously, in order that waste by leaching may not result.

It is important in maintaining phosphates in available form, and in counteracting the injurious effects of many substances in the soils, including certain products of fertilizers. In many ways it has an intimate relation to the nitrogen supply of plants, for it promotes the formation of nitrates from organic matter, diminishes the destruction of these, and seems to be generally almost indispensable for the proper development of the nitrogen-fixing root-tubercle organisms.

The above effects may be considered those of most intimate consequence for plants generally; but in addition it may improve (by flocculation) heavy soils, and it may be important as an insecticide and a fungicide (although it is favorable to potato scab and to root rot of tobacco).

96. Iron. — A certain amount of iron seems to be necessary as one of the factors in the normal development of leaf green, or chlorophyll, although it is not regarded as a constituent of the organic bodies which make up this substance. Lack of iron is one of the many conditions leading to pathological chlorosis. It may be that the lack of iron affects the protoplasmic structure (the plastid) in which the chlorophyll is deposited, for the best evidence points to the use of iron by every living cell, including, therefore, those organisms which contain neither this pigment nor any allied compounds.

In cases where iron is deficient in the soil, or held as markedly insoluble compounds, beneficial results have been obtained by the application of a soluble salt. Richards and Ono have shown that iron salts have a remarkably stimulating effect upon filamentous fungi, increasing the dry weight several fold over that obtained when the minimum used is merely that which would occur as impurities in the purest salts. Final proof of the relation of diverse plants to iron is most difficult to obtain, owing to the presence of traces of this metal in many of the purest salts.

97. Sodium. — Sodium, a metal indispensable in animal nutrition, is not required by plants. It would seem that it may at times prove beneficial, and in the field relations of crops it is often indirectly serviceable by setting free other requisite bases. Breazeale has shown, by experiments interesting both with respect to method and result, that more sodium is absorbed, and that it may be directly beneficial, in the absence of sufficient potassium.

Wheeler has conducted extensive field experiments, upon various aspects of the sodium problem. This work supports the views advanced, in a measure. It also indicates that field applications of sodium may be beneficial in subsequent years "in those cases where the previous application of potassium salts had been large." He regards this as "due, in part at least, to the retention in the soil of a part of the previous applications of potassium salts, by virtue of extra soda having been taken up by the preceding crops in the place of superfluous potash, whereby the potash supply in the soil was really conserved."

98. Chlorine. — Chlorine seems to be generally inessential for the complete development of the higher plants.

Knop and other students of nutrition so regarded it, and it is sometimes omitted from the nutrient solution. It is an invariable constituent of the soil solution, and either on this account, or in the belief that it is generally somewhat advantageous, it is commonly added to the nutrient ration as NaCl or KCl.

Nobbe and others have found KCl indispensable in the proper maturity of buckwheat, which, deprived of it, develops a pathological condition at or following the period of flowering, resulting in a failure to form seed. A light fertilization of special crops with sodium chlorid has not infrequently resulted in increased yield; but in most cases it is not certain that the action is direct, and even less clear that it is the additional chlorine which is important in the substance employed. This relation of plants to chlorine is the second notable difference in the metabolism of plants and animals.

99. Sulfur. — Sulfur is primarily important because of the fact that it is contained in albuminoidal compounds. It occurs in some of the by-products of protein production, and also as sulfates of the bases — especially potassium — occurring in the cell-sap. It is usually required in such limited quantity that the seed may furnish all that is needed for the normal growth of the plant through a considerable period.

100. Silicon. — Silicon forms a predominant part of the ash of many grasses and other plants. It accumulates in old stems and caulms, and may constitute from 40 to 70 per cent of the ash of cereal straws and corn stover. Nevertheless, corn may be grown without any further addition than that furnished by the seed. One of the

species of the scouring rush (Equisetum) has an ash content of SiO_2, amounting to from 70 to 80 per cent. The accumulation is chiefly in the cell-wall, where it is doubtless important in support and protection. Silicon is regarded as an inessential element because development proceeds in its absence; but in the complex relations of plants in the field it may determine the capacity of a plant to exist in a particular habitat. Wolff regarded silicon as important in furthering the migration of phosphoric acid compounds from maturing leaves and stems to the forming seeds.

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BALANCED SOLUTIONS

Since the early studies upon the mineral nutrients of plants, it has been more or less apparent that any one of the nutrient salts employed singly may be injurious, or may inhibit growth. The extent of this inhibition of growth has in recent years been more extensively measured. Moreover, it has long been realized that in the preparation of the nutrient solution a certain ratio of the different salts is required, or may be favorable, for the best results.

It is now known that there are certain interesting antagonistic relations between some of the nutrient and other bases whereby the inhibitory effects of one may be in part or entirely counterbalanced by the presence of another. A solution in which the inhibitory or toxic action of one substance is rather effectually eliminated by an "antagonistic" compound is now generally termed a balanced solution. Some cases of alleged antagonism are apparently complicated by factors of nutrition and exosmosis, but at present it is not possible to evaluate the different factors.

101. The injurious action of certain basic nutrients. — Although toxic action in general is discussed at length later, it is necessary here, in connection with balanced solutions, to note the relations of some plants to some of the several single nutrient compounds. The following table, from data by Kearney and Harter, shows approximately the limiting concentrations of two sodium and two magnesium salts, endured for twenty-four hours by wheat, lupine, and maize: —

Salt	Wheat		Lupine		Maize	
	Parts of a Normal Solution	Parts per 100,000 of Solution	Parts of a Normal Solution	Parts per 100,000 of Solution	Parts of a Normal Solution	Parts per 100,000 of Solution
Magnesium sulfate	.007	39	.00125	7	.25	1400
Magnesium chlorid	.009	108	.0025	12	.08	394
Sodium sulfate . .	.043	302	.0075	53	.05	353
Sodium chlorid . .	.054	313	.02	116	.04	232

In general, the magnesium compounds are particularly toxic to the higher plants. Corn is an apparent exception to the rule, as are also most fungi and some algæ. On account of the fact, then, that magnesium compounds are so generally harmful when alone, or in relative excess, it is of special interest to note in some detail the relation of this element to other bases.

102. The relation of calcium to magnesium. — The toxic action of magnesium and the effect of calcium in modifying it were established by Von Raumer in 1883; but the most important work in outlining and directing attention to this field with respect to plants was done by Loew and his associates. There is at present a mass of data available both on the plant and on the animal side. As a general result of all the work on the higher plants it is now clear that when magnesium is injurious, the presence of calcium in a certain ratio (variable for the plant) destroys this toxicity entirely. To explain this relation Loew formulated his theory of the existence of a calcium-protein body as previously outlined (section 95).

The lime-magnesia relation in the soil is, moreover, of much practical importance, and it is certain that when magnesia is relatively abundant in soils there is usually need of liming. Under such circumstances it is obvious that the application of a dolomitic limestone (rich in magnesium) should be avoided. The evidence upon this point is also extensive. There are practical difficulties, however, in determining the proper ratio of CaO : MgO in the soil, for the question of availability must be considered. Water culture and pot experiments have suggested such differences in the requirement of plants as shown by the following favorable ratios: —

Buckwheat	CaO to MgO	3 to 1
Cabbage	CaO to MgO	2 to 1
Oats	CaO to MgO	1 to 1

Loew believes that the greater the leaf surface produced in a given time, the greater the necessity for lime; that is, the higher the ratio. In this connection it is shown that with respect to the lime requirement the need of tobacco, clover, grass, sugar-beet, and wheat form a decreasing series. The cereals never show a ratio higher than 2 : 1. In solution cultures in the laboratory the effect of the omission of calcium from a solution containing magnesium, or the inappropriate ratio of calcium, results in a markedly decreased growth. In the following chart, giving the effect of the calcium-magnesium ratio upon the growth of the Canada field pea, this fact is made clear,[1] the

[1] These data correspond to the series of cultures in Figure 51, and are from careful laboratory experiments by graduate students.

single average plant being taken as the basis of the diagram, — each major ordinate denoting .1 gm.: —

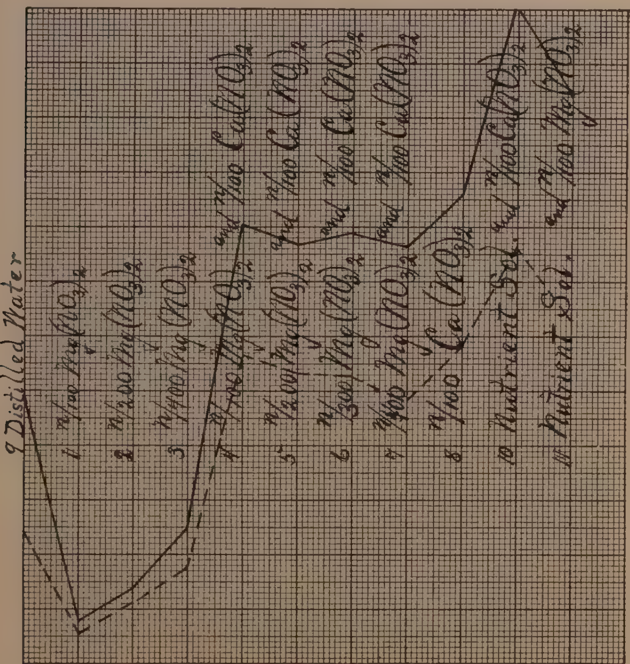

FIG. 50. Antitoxic action of calcium and magnesium nitrate; curves of total green weight (unbroken line) and green weight of stem (broken line).

In the cultures diagramed above the whole period of growth is 17 days. The original quantity of the solution was maintained by replacing with distilled water the loss by transpiration; but after 14 days all solutions were

completely renewed. For such a period of growth the seeds of the pea carry a fairly adequate supply of the other nutrients. Again, the seed is relatively rich in magnesium, so that the omission of this element affects growth very slightly, while the same fact emphasizes the need of calcium in the solution.

103. Other nutrient bases and antitoxic action. — The neutralizing action of various bases upon one another has been demonstrated by Loeb, Kearney, Osterhout, and others. In this regard calcium is most important. At suitable concentrations it reduces the toxicity of deleterious solutions containing either potassium, sodium, or ammonium, as well as of certain nonnutrient bases.

The table on the opposite page includes data furnished by McCool[1] from two distinct series of cultures with the Canada field pea grown 30 days.

In the first series the concentration of sodium employed shows no growth whatever, and the addition of one fortieth as much calcium gives a very considerable growth; therefore, a marked antitoxic effect. The best growth occurs where the stronger concentrations of calcium are used with the sodium, so that there appears to be a slight mutual antagonistic action with respect to peas. The strong effect of calcium upon the relatively toxic ammonium salt is apparent.

In general, all of the nutrient bases show a series of relations with respect to toxic action upon plants. For each base the relations may be different, and a certain variability is to be accounted for by differences in the composi-

[1] The experiments of which these constitute a small part will be published as a bulletin of the Cornell Experiment Station.

ANTITOXIC ACTION — CANADA FIELD PEAS

Solution Cultures Contain	Average Length of 10 Plants		Green Wt. in Grams of the 10 Plants	
	Tops, in cm.	Roots, in cm.	Tops	Roots
$\frac{N}{1000}$ $CaCl_2$	22	13	6.2	3.3
$\frac{N}{2000}$ $CaCl_2$	18	10	5.1	2.2
$\frac{N}{4000}$ $CaCl_2$	19	9.5	4.8	2.1
$\frac{N}{100}$ $NaCl$	no growth	no growth	no growth	no growth
$\frac{N}{1000}$ $CaCl_2$ and $\frac{N}{100}$ $NaCl$	18	12	5.25	3.9
$\frac{N}{2000}$ $CaCl_2$ and $\frac{N}{100}$ $NaCl$	25	14	6.5	4.6
$\frac{N}{4000}$ $CaCl_2$ and $\frac{N}{100}$ $NaCl$	17	11	4.8	3.7
Distilled water	7	3	2.2	1.8
$\frac{N}{100}$ $CaCl_2$	13	8	——	2.85
$\frac{N}{2000}$ NH_4Cl	4	no growth	——	no growth
$\frac{N}{3000}$ NH_4Cl	4	no growth	——	no growth
$\frac{N}{4000}$ NH_4Cl	4	no growth	——	no growth
$\frac{N}{100}$ $CaCl_2$ and $\frac{N}{1000}$ NH_4Cl	9	7	——	2.0
$\frac{N}{100}$ $CaCl_2$ and $\frac{N}{2000}$ NH_4Cl	11	8	——	2.0
$\frac{N}{100}$ $CaCl_2$ and $\frac{N}{3000}$ NH_4Cl	10	8	——	2.54
$\frac{N}{100}$ $CaCl_2$ and $\frac{N}{4000}$ NH_4Cl	10	8	——	2.03
Distilled water	7	3	——	1.8

FIG. 51. From a photograph of the cultures embodied diagrammatically in Fig. 50, the numbers corresponding.

tion or absorptive action of the plants used as indicators. Moreover there is diversity in the visible results of the toxic action by the different nutrients; thus salts of ammonium kill the roots before the shoots are noticeably affected, while sodium salts kill the shoot promptly. It is important that there is toxic action, and that there may be antagonistic or mutually antagonistic action.

An entirely satisfactory explanation of these phenomena is not at present available. Loew's views on the calcium-magnesium relation are strengthened by the opinions of Loeb and others who postulate in organisms a number of metal proteins, so that any solution containing only one class must be ultimately toxic. Even this view is not sufficiently broad to account for all of the known facts; for example, the antagonism between inessential and essential ions.

LABORATORY WORK. — SUGGESTED EXPERIMENTS

Injurious action of single nutrients. — After consulting the literature of the subject determine the concentrations of $MgCl_2$, $CaCl_2$, KCl, and NH_4Cl, which when used separately will just permit the growth of roots of wheat or peas. Employ ten plants in tumblers or bottles, as in the nutrition studies.

Balanced Solutions. — Guided by the indications given under nutrient solutions regarding manipulation, set up the experiments outlined below, employing in each culture wheat or Canada field peas. Prepare stock cultures of $\frac{N}{50}Ca(NO_3)_2$, $\frac{N}{50}Mg(NO_3)_2$, $\frac{N}{100}NaCl$, $\frac{N}{100}CaCl_2$, also double strength of nutrient solution; from these prepare, by dilution, all the following cultures, also employing distilled water as a check: —

CALCIUM *versus* MAGNESIUM

	Use	Solution Contains
1.	125 cc. $\frac{N}{50}$ $Ca(NO_3)_2$. 125 cc. distilled water.	$\frac{N}{100}$ $Ca(NO_3)_2$.
2.	125 cc. $\frac{N}{50}$ $Mg(NO_3)_2$. 125 cc. distilled water.	$\frac{N}{100}$ $Mg(NO_3)_2$.
3.	50 cc. $\frac{N}{50}$ $Mg(NO_3)_2$. 200 cc. distilled water.	$\frac{N}{250}$ $Mg(NO_3)_2$.
4.	25 cc. $\frac{N}{50}$ $Mg(NO_3)_2$. 225 cc. distilled water.	$\frac{N}{500}$ $Mg(NO_3)_2$.
5.	125 cc. $\frac{N}{50}$ $Ca(NO_3)_2$. 125 cc. $\frac{N}{50}$ $Mg(NO_3)_2$.	$\frac{N}{100}$ $Ca(NO_3)_2$ and $\frac{N}{100}$ $Mg(NO_3)_2$.
6.	125 cc. $\frac{N}{50}$ $Ca(NO_3)_2$. 50 cc. $\frac{N}{50}$ $Mg(NO_3)_2$. 75 cc. distilled water.	$\frac{N}{100}$ $Ca(NO_3)_2$ and $\frac{N}{250}$ $Mg(NO_3)_2$.
7.	125 cc. $\frac{N}{50}$ $Ca(NO_3)_2$. 25 cc. $\frac{N}{50}$ $Mg(NO_3)_2$. 100 cc. distilled water.	$\frac{N}{100}$ $Ca(NO_3)_2$ and $\frac{N}{500}$ $Mg(NO_3)_2$.
8.	125 cc. $\frac{N}{50}$ $Ca(NO_3)_2$. 125 cc. nutrient sol.	$\frac{N}{100}$ $Ca(NO_3)_2$ and nutrient sol.
9.	125 cc. $\frac{N}{50}$ $Mg(NO_3)_2$. 125 cc. nutrient sol.	$\frac{N}{100}$ $Mg(NO_3)_2$ and nutrient sol.
10.	Distilled H_2O.	Distilled water.

The above series should show toxicity of the magnesium salt and antagonism.

In the same manner as for the preceding prepare solutions to contain the following: —

11 and 11*a*. $\left\{\begin{array}{l}\frac{N}{25}\,CaCl_2.\\ \frac{N}{100}\,CaCl_2.\end{array}\right.$ 12. $\frac{N}{2500}\,CaCl_2$. 13. $\frac{N}{100}\,NaCl$. 14. $\frac{N}{2500}\,NaCl$.

15. $\frac{N}{25}\,CaCl_2$ and $\frac{N}{100}\,NaCl$.

16. $\frac{N}{25}\,CaCl_2$ and $\frac{N}{2500}\,NaCl$.

17. $\frac{N}{2500}\,CaCl_2$ and $\frac{N}{100}\,NaCl$.

18. $\frac{N}{2500}\,CaCl_2$ and $\frac{N}{2500}\,NaCl$.

19. $\frac{N}{25}\,CaCl_2$ and nutrient sol.

20. $\frac{N}{100}\,NaCl$ and nutrient sol.

Permit the plants to grow under favorable conditions fourteen days, supplying distilled water as needed by transpiration. Discuss the results, tabulate data on length and green weight; also plot curves of the total green weight in the two series.

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CHAPTER IX

THE INTAKE OF CARBON AND THE MAKING OF ORGANIC FOOD

ORGANIC matter constitutes the predominant part of the solid constituents of plants. As organic matter so-called, this element is linked chiefly with hydrogen; with hydrogen and oxygen; with hydrogen, oxygen, and nitrogen; or with the preceding and one or more of the essential mineral elements. Nevertheless, carbon may be regarded as the significant element of organic compounds. The number of such organic compounds in plants and animals and their products is almost beyond count. It is the special province of organic chemistry to deal chemically with these carbon series, but some account of the origin, nature, and rôle of certain of these substances in the living organism is a most important part of physiology, whether elementary or advanced.

104. The amount of carbon in the plant. — We have noted the relatively small amount of mineral or ash elements in plants, constituting usually from 1 to 5 per cent of the total weight of the water-free substance. Nitrogen adds a further fraction, — seldom more than 5 per cent, — and the remainder, that is, more than 90 per cent of the dry matter, is made up of carbon, hydrogen, and oxy-

gen. A crude picture of the distribution and importance of the carbon in plants is afforded by the well-known process of charcoal making, — a burning without free access of oxygen. As a result, the hydrogen, nitrogen, and oxygen of the plant are set free, while only carbon and the small proportion of ash remain. When burned with abundant oxygen, the carbon combines with the oxygen by an oxidation or hydroxylation process, and gaseous carbon dioxid is ultimately formed. In this case a perfectly definite amount of energy, as heat, is released.

105. Carbon dioxid the source of carbon in green plants. — We are now concerned with the source from which plants obtain their carbon supply, the conditions of intake, and the method by which the carbon is incorporated into food for the plant cell. Carbon in inorganic form, especially as carbonates of lime and magnesia, constitutes no inconsiderable portion (about twice as much as phosphorus) of the minerals of the earth's crust. Yet, as will be subsequently indicated at length, carbonates are valueless as a source of the carbon from which to make organic compounds for either plant or animal. Moreover, both water and sand cultures abundantly demonstrate that green plants are able to grow and to attain their full development (necessitating the making of organic matter) in nutrient solutions containing no carbonates and also no organic matter whatsoever save that derived from the seed.

It is easy to convince ourselves of the requirements of common animals with respect to organic matter. They feed upon plants or other animals, or upon the products of these. Moreover, there are the countless fungi and

bacteria (with marvelously few exceptions[1]) familiar as molds, plant parasites, mushrooms, organisms of decay, and of various fermentative processes; these all require an intake — from without the body — of organic carbon nutrients. Organisms which thus obtain their carbon as organic matter, and which have no apparatus for making it from carbon dioxid and water are in the end dependent. Such organisms have also been termed heterotrophic. Green plants are practically alone in being able to make organic matter out of the raw materials, carbon dioxid and water; they are independent. Conveying the idea that they make organic food somewhere within the body, and in the first instance for their own use, they have been called autotrophic.

106. Chlorophyllous plants. — So far as is known, green plants have always supplied the earth with organic matter, including fuel. The leaf-green which they contain is the strongest link binding living things to the sun, — the one ultimate source of radiant energy available upon the earth. The means whereby this making of organic food is accomplished is fundamentally important, and requires careful consideration. All living processes and phenomena are important, but since this stands out as the method whereby the world's supply of organic matter is made, the process assumes an interest scarcely second to that of life itself.

The green or yellow-green color, sometimes partially veiled, is practically universal among plants which we now recognize as possessing the highest type of plant habit

[1] The exceptions consist in a few species of bacteria, subsequently discussed (section 128), whose paltry contribution to the stupendous quantity of organic matter existent is such as to be wholly negligible.

and form. It characterizes also to a very high degree the algæ and mosses, but it is absent from all the fungi. Several facts regarding the habitats and distribution of green plants afford us an indication of some of the conditions requisite for the proper work of plants thus endowed. The presence of the green color referred to is universally indicative of the possession of chlorophyll, a mixed pigment, imbedded in certain chloroplasts, or chlorophyll containing bodies which are differentiated portions of the living protoplasm. In particular, it is apparent that plants containing this substance are sun-loving or at least light-loving organisms. They may grow in partial shadow at times, but they are wholly absent from all permanently dark or deeply shaded places. The large surfaces of the leaves and the evident arrangement of these and of the branches which bear them, with respect to light, all indicate clearly a certain relation of green color with the light factor. As the chief bearers of chlorophyll in seed-plants the leaves command special attention, wholly aside from their other functions or accessory work. Any agency

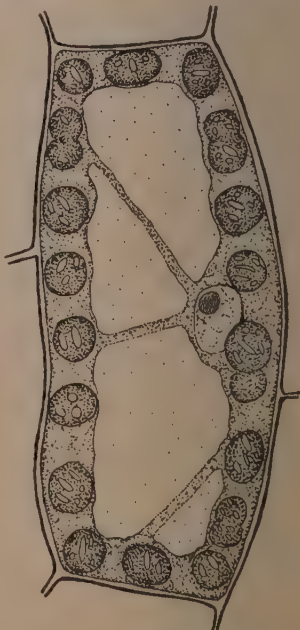

FIG. 52. Cell of chlorenchyma showing chloroplasts with starch grains. [Adapted.]

Fig. 53. A leaf mosaic as exhibited by the grape-vine.

affecting their health injuriously, such as insect pests, fungous diseases, general unfavorable environment, ac-

FIG. 54. Abutilon, side view, under greenhouse illumination.

cumulation of dust or soot thereon, means restriction of their work in production.

107. Respecting the distribution of chlorophyll. — In the higher plants the chlorophyll bodies may be disposed in

all exposed vegetative organs, but the leaves are primarily the seats of their occurrence. The palisade and general parenchyma cells of the leaf ordinarily contain many

FIG. 55. Abutilon ; looking down upon the plant shown in Fig. 54.

chloroplasts (Fig. 25). Such tissue is designated chlorenchyma. In stems or other thick organs the chlorenchyma is comparatively near the surface; for, as a rule, the formation of chlorophyll is directly or indirectly dependent

upon light. Notice the color of seedlings which have grown in the dark and of grass beneath a board or pile of leaves. The epidermal cells of seed-plants are commonly colorless, yet the guard cells of the stomata are important exceptions. Nevertheless, there are certain structures which, supplied with a good food-supply, contain chlorophyll, even when produced in the dark; for example, the cotyledons of pine.

The white or yellow areas of variegated leaves may contain no chlorophyll; but leaves which are during growth brown, red, or otherwise highly colored contain chlorophyll bodies, the color in such cases being veiled by the presence of other pigments often present in the cell-sap. The diverse pigments of many algæ exhibit a greater complexity. In the great majority of plants the chlorophyll bodies are discoidal or button-like forms (often lenticular or more nearly plano-convex), although in certain of the algæ (Spirogyra, desmids, etc.) they may possess unusual peculiarities of shape. The intimate structure of the chloroplast is none too well known. Briefly, it may be said that there is a cytoplasmic stroma, and within this is contained the green pigment, somewhat diversely deposited in different cases.

108. The nature and properties of chlorophyll. — By means of alcohol, chlorophyll may be extracted from plants, leaving the tissues practically white. Either ethyl, methyl, or denatured alcohol may be employed, and the process is greatly facilitated by carefully bringing the alcohol to a temperature close to its boiling point over a water-bath. Seedling plants of the horsebean, small cereals and grasses, radish, or nasturtium afford as favorable

solutions as may be conveniently obtained. The solution is fluorescent by reflected light, and it is rapidly decomposed in strong light.

The chlorophyll pigment as extracted is a mixed substance. Two products which are constant and predominant permit of partial separation through their diverse relations to solvents. Thus if benzole is added to the alcoholic solution and the latter vigorously shaken, there will result on standing a blue-green benzole layer and a yellow alcohol layer. There are therefore two substances, a blue-green one which has passed largely into the benzole, and from the color it is usually called blue chlorophyll or cyanophyll; while the yellow substance remaining in the alcohol is mostly carotin.

Apparently cyanophyll does not exist alone in nature. It is a complex molecule containing nitrogen, and is variously supposed to have phosphorus or magnesium associated or combined with it. Cyanophyll is closely related, it would seem, to the hæmoglobin of blood; and it yields a variety of decomposition products, some of which colorimetrically and chemically seem to be identical with certain products of hæmoglobin.

Carotin is of common occurrence in a variety of colored tissues, and in its crystalline form it is most conspicuous in the root of the carrot and in the petals of certain orange or yellow flowers. This pigment belongs to the group often called xanthophyll. The term "etiolin" is also applied to it. The substance is present in etiolated organs, and it may long persist in the chloroplasts of leaves during the autumn.

The most important property of chlorophyll is its ca-

pacity to absorb light, that is, radiant energy to which the retina of the eye is sensitive. The relation of the chlorophyll and of its main constituents to the absorption of light of different wave lengths, as shown by a spectroscopic examination, is discussed later. The radiant energy absorbed by the chlorophyll is the force operative in photosynthesis.

109. The factors essential in photosynthesis. — We may now review briefly the essential features of the process whereby chlorophyll-containing plants in the presence of light are able to construct organic food-materials. The process is termed photosynthesis. In order that photosynthesis may proceed in the cells of healthy plants, it is necessary that light shall fall upon chlorophyll bodies in the presence of aqueous carbon dioxid. Temperature and other factors are important, — the exact relation to temperature being especially difficult to analyze, — and in general the process is possible only within a certain range of physiological conditions. Nevertheless, under ordinary conditions of growth we may regard as the primarily essential factors: (1) chlorophyll, (2) light, and (3) carbon dioxid, the last two of which will receive further consideration later.

110. The course of photosynthesis. — Briefly stated, the gas exchange and the actual phases (several of which are more or less simultaneous) of the process of photosynthesis as commonly conceived are as follows: —

1. Gas exchange between the green tissues and the surrounding air, whereby carbon dioxid may be absorbed by the cell-sap and reach the protoplasm.

2. The absorption of radiant energy, as light, by means of the chlorophyll bodies.

3. The use of this kinetic energy in the decomposition of carbon dioxid and water ($H_2O + CO_2$, or H_2CO_3), the synthesis of an elementary organic product, and the consequent storage of potential or latent energy.

4. The probable condensation of the synthate into a carbohydrate of high food value, generally fruit sugar, which is then often in part transformed into starch.

5. The elimination, by gas exchange, of O_2, a by-product of the process (some of which, however, may be used in respiration, subsequently treated).

It is seen, therefore, that there is a physical mechanism for gas exchange, a series of transformations of energy and of compounds, and ultimately the deposition of food-materials, frequently starch. It is now necessary to consider a method of demonstrating this process, and later there will be required a further consideration of the course of events, the factors involved, the energy transformations, and some of the products resulting.

111. The demonstration of photosynthesis. — It is possible to demonstrate photosynthesis in any plant more or less completely by one or more of several methods, and no single simple experiment will reveal all the facts desired. With all other factors well controlled,[1] increase in weight, or the accumulation of some organic product (especially starch) are practicable demonstrations. Another type of experiment involves, when accurate, an analysis of the gas used, or that eliminated, or both; but such eudio-

[1] The student who may pursue this matter farther should examine carefully the difficulties and beauties of well-controlled experiments; consulting Ganong's "Plant Physiology" (2d Ed.), pp. 79–114; also the earlier account in Sachs.

metric methods should be carried out in an accurate manner by the use of special apparatus.

For demonstration purposes the evolution of oxygen from cut stems of water plants (such as Elodea or Cabomba) is the simplest indication of photosynthesis; but this may not be applied to land plants. During photosynthesis gas escapes from the large air chambers through the cut stems, and with vigorous action a slow stream of bubbles may arise. It is then necessary to employ a method whereby these bubbles may be caught so that the gas may be simply identified.

A funnel may be inverted over a quantity of clean, growing sprigs of Elodea, or water weed, in a deep vessel or aquarium. Over the funnel is inverted a test-tube of water (Fig. 58) for the collection of the oxygen. In order that there may be free access of carbon dioxid, the funnel should be much smaller than the vessel and should rest on supports several inches above the bottom; while the water should be spring or well-aërated tap water, or should contain a supply of CO_2 introduced from a generator. The gas caught in the tube may be tested by proper manipulation (see Laboratory experiments, p. 221), with an oxygen absorbent, preferably pyrogallate of potassium.

If the gas is collected under favorable conditions, it will consist largely of oxygen, — about four fifths; the remainder consisting of other gases formed in the plant and of nitrogen from the air, which must, of course, diffuse into the air spaces. Having determined that oxygen is the chief part of the gas given off as bubbles from water weeds, during photosynthesis, the simple bubble-counting method may be employed in determining relatively the rate of

photosynthesis with different intensities and quantities of light, with varying quantities of CO_2 (up to the saturation point of water), at various temperatures, etc.

112. The formation of sugar and starch. — With respect to the formation of organic food-material it has been indicated in the brief outline of the course of photosynthesis that glucose is generally regarded as the first stable result. The formation of glucose and free oxygen from carbon dioxid and water constitutes a complex process, but the reaction is commonly expressed in the following conventional manner: —

$$6\ CO_2 + 6\ H_2O = C_6H_{12}O_6 + 6\ O_2.$$

Some years ago the view was advanced by Von Baeyer that formaldehyde is an early step in the reduction of the carbonic acid, and that then six molecules of the formaldehyde, $H \cdot COH$, become linked together or condensed to form a hexose sugar, $C_6H_{12}O_6$. Recent work along many lines strengthens this conception of the process, and it seems to have been demonstrated (although there are some criticisms of the method) that by artificial experiments with the factors light, chlorophyll, and CO_2, formaldehyde may be produced, although in small amount as compared with the quantity which must result from photosynthesis. The details of this work, however, and the criticisms thereof do not require consideration.

It is difficult to picture simply all possible relations of the glucose which may appear as the first stable product, but the accumulation of this substance in the cell leads to the formation of other sugars, especially bioses ($C_{12}H_{22}O_{11}$) and ultimately to starch, a complex molecule having the general formula $(C_6H_{10}O_5)_n$.

Starch then is an accumulation product apparently conditioned only when the tension of the sugar which has been produced is considerable, at least so considerable that the cell is unable to use the surplus in building up the permanent structures, or to remove it fast enough. Starch is deposited within the chloroplasts in the form of small granules. During the growing season it normally accumulates in most leaves through the day, or so long as the leaves are exposed to strong light; while during the photosynthetic inactivity of the night much or all of this starch may be removed. In most cases the leaf will be depleted of starch if placed in the dark for a period of 12 hours, if the leaf is not in itself a storage organ. The process of starch removal and subsequent deposition, when that occurs, invites special consideration later.

In those plants forming starch abundantly in the leaves it is often desirable, and extremely convenient, to employ the relative accumulation of starch as a rough qualitative indication of photosynthetic activity. Leaves from which chlorophyll has been extracted may be stained with a weak alcoholic solution (tincture) of iodine, the leaves being preferably placed on a white plate to be stained. When added to a weak suspension of starch, or to a weak starch paste, iodine yields an intense blue or blue-black color. Starch in the leaf, or in other tissues, is, however, considerably obscured, and it often gives a blue-brown or even brown-black reaction. Plants of the iris, lily, amaryllis, and orchid families form, as a rule, little or no starch.

113. The diffusion process. — It has already been shown that the leaf (or an analogous structure) is an ad-

mirable device to permit rapid diffusion with a minimum direct exposure of delicate cells. Uncutinized surfaces are moist and may absorb CO_2 directly, but the epidermis is usually cutinized, and therefore it is through the stomata largely or entirely that a constant gaseous diffusion takes place between the air spaces of the leaf and the external atmosphere. The epidermis is an effective multiperforate septum, which means that, with a difference of gradient within and without, the relatively small stomatal areas are far more efficient in diffusion than would be suggested by their actual area. They are in fact sufficient to provide for the maximum diffusion of CO_2 which may take place from a natural atmosphere into the plant.

The CO_2 which enters the air chambers of the leaf is rapidly absorbed by the moist cell-walls within. These cell-walls absorb the carbon dioxid just as would any membrane moistened with water. The above capacity for absorption is so great that there is during photosynthesis practically no tension of CO_2 in the air spaces. The carbon dioxid in solution is presented by the cell-sap to the chloroplast, and there is, of course, continuous absorption and migration through diffusion in solution, so long as photosynthetic action proceeds. The CO_2 absorbed does not immigrate to any considerable distance before it is used. This is easily demonstrated by the fact that in small darkened areas no starch would be produced. It must be transferred, in some leaves, however, as far as the upper palisade layers, for in these there is usually abundant starch-making. It is apparent that in general the sphere of each stoma is more or less local. The intake of carbon dioxid is greatest, usually, over the lower surface of the

leaf, and there the air chambers are most numerous; but chlorenchyma is better developed toward the upper surface. There are, however, so many factors which influence the structure of the leaf that the apparent inconsistency of this arrangement must be regarded as an effective compromise.

The same stomatal mechanism effects, of course, a rapid elimination of the oxygen produced during photosynthesis, after this oxygen has diffused into the air spaces from the moist membranes of the cells wherein it is produced.

114. The amount of carbon dioxid. — The amount of carbon dioxid in the air seems almost infinitesimal when we contemplate the results of its use. The air contains normally about .028 to .03 per cent, although this amount may be temporarily somewhat increased in the neighborhood of cities, or of areas where manufacturing is a chief industry. The limited amount of this gas suggests, further, the necessity of broad surfaces and the thorough distribution of chlorophyll.

It has been found that the normal supply of carbon dioxid is often insufficient for the maximum work of the leaf. Under ordinary conditions, as when the plant is growing in strong light at a temperature of from 20 to 25° C., and with a sufficient water-supply, a chief limiting factor in growth is the minimum tension of carbon dioxid.

It has been shown experimentally that an increase in the amount of this gas to such extent that the air will contain from 1 to 10 per cent or more may be beneficial, provided the other factors permit a maximum activity. The results obtained by Godlewski and Kreusler are not entirely

concordant, but sufficiently so to indicate that the curve representing photosynthetic activity rises rapidly as the content of CO_2 is increased to an air content of from .1 to 1 per cent, and subsequently the rise, if continuous, is slow to about 10 per cent, after which it may decline.

The amount of CO_2 in the present atmosphere of the earth is sufficient for all the needs of plants throughout imaginable time. It must be assumed, indeed, that this amount will never be much more or much less than at present, and that, practically speaking, the forces governing supply and demand are ultimately somewhat regulatory; although there is geological evidence that atmospheric CO_2 has not been constant. The result of all animal and plant respiration (see Respiration, p. 280) is to return to the air daily an enormous quantity, — an amount estimated for mankind alone to be not less than 50,000,000 tons. The great present consumption of fuel — coal, wood, oil, etc. — returns to the air several billion tons every year. A moment's consideration of the production of coal in the United States alone during 1907 (400,000,000 tons yielding about 2 times this amount of carbon dioxid) is alone sufficient to indicate the immensity of the quantities which are involved in these exchanges. This coal represents in part, of course, the photosynthetic activity of plants of the carboniferous age. In addition to these sources of CO_2 there is also the disintegration of rock carbonates.

With rapid circulation of air the CO_2 of the atmosphere is evenly distributed throughout, and plants, tall and low, are in situations equally favorable. When, however, the atmosphere is quiet, there is, especially in rich ground,

rapid diffusion of CO_2 from the soil, due largely to the activity of microörganisms of the soil. In consequence there may be a stratum near the soil so much richer in CO_2 as to be distinctly advantageous for low-lying or rosette-forming plants.

115. Light the source of energy. — It has been indicated that an important feature of the work of chlorophyll is the absorption of light, or the taking over of energy. If a beam of sunlight is dispersed by a suitable prism, it is found to consist of groups of rays of different wave length, refrangibility, and "color"; the beam is thus separated into the well-known spectrum, the visible portion of which presents a series of colors as follows: red, orange, yellow, green, blue, indigo, and violet.

If in the path of light there is interposed a weak solution of chlorophyll in a suitable glass vessel, certain definite absorption bands appear in this spectrum. There are, in fact, seven of these, four in the region of red to green and three beyond the blue, generally rather indistinctly demarcated, and in strong solutions cutting out the visible rays beyond the blue (Fig. 56). The four bands in the red end of the spectrum are those of the blue-green solution, cyanophyll; and the most important absorption band is in the red, corresponding to wave lengths of 650 $\mu\mu$ and thereabout.

A considerable amount of experimental work has been done to determine the rate of photosynthesis under the different monochromatic lights. Colored glass screens and double-walled vessels containing colored liquids have been much employed. Since such materials seldom afford pure monochromatic lights, they give only a crude idea of

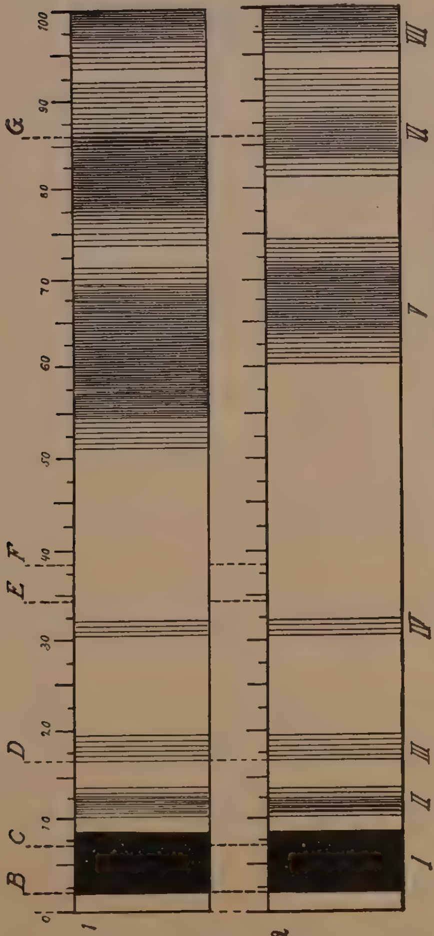

FIG. 56. Absorption spectrum of chlorophyll. [Adapted.]

the relative effects of light quality. Experiments of this nature are important, especially when the light employed is analyzed as to its energy value. It can be shown that bubbles of oxygen are more rapidly given off, or starch is more rapidly formed, under red-orange screens than under green or blue. Red light is therefore a chief source of the energy used in food-making.

116. Efficiency of the food-making apparatus. — Painstaking and brilliant investigations have been made upon the energy relations of leaves. The work of green plants is truly remarkable, and it is impressive to consider these organisms as the noiseless machines engaged in the manufacture of all that organic material upon which life depends — the foremost conservators of the energy derived from

Fig. 57. Ganong's simple light-screen and aërated box for showing the necessity of light in starch-making.

sunlight. When, however, it is asked how economic or efficient is this world-distributed apparatus with respect to the energy received, one experiences at first a keen disappointment to ascertain that the highest estimates indicate an effectiveness of only 3 per cent, and, according to other estimates, it may be as low as .5 per cent. Still, the amount of light absorbed by the leaf is considerable, and it is important to note the result of this.

In diffuse light the leaf may absorb 95 per cent falling upon it, while in direct light only about one half is absorbed, or reflected. In either case much of this absorption is due to the chlorophyll bodies which have a capacity of from 10 to 20 times or more the amount effective in actual photosynthesis. The surplus energy absorbed is in part operative in raising the temperature of the leaf, which, according to Blackman, may be in direct sunlight from 10 to 15° C. higher than that of the surrounding air. This surplus, of course, induces a more intensive evaporation. Perhaps if we knew more of the physical and chemical changes involved in food-making, this efficiency would be unchallenged.

116a. Light, intensity and quality. — The relation of food manufacture to the intensity and quality of light is most complex. Under favorable conditions of temperature the working capacity of many plants is proportional to the increase in light intensity, at least up to the point where the available CO_2 is not a limiting factor. Nevertheless, experiments made from another standpoint indicate that with respect to photosynthesis under field conditions there are shade-loving plants — plants which seem to be thoroughly attuned to a maximum capacity for

food-making in weaker light. In this connection, however, it is possible that an important factor limiting high production in intense light is the increased evaporation then resulting, which would tend to dry out the plant and induce a closure of the stomata, as well as otherwise affect photosynthesis. The control of light intensity is important in crop work, as more particularly discussed under shading.

116b. **Temperature.** — Temperature is just as important in food-making as in any other physiological process. According to Blackman the best temperature for sustained photosynthesis is generally about 25 to 30° C., and this in spite of the fact that at a temperature of about 10° the cell-sap may absorb and hold practically twice as much CO_2 as at the former temperature. The effect of higher temperatures upon respiration complicates the heat relation. It may be expected that plants adapted to diverse environmental conditions will not respond alike to heat, especially under field conditions. High temperature is an important factor in the early maturity of wheat. The grain then contains relatively little starch, and the yield of straw is lessened. On the other hand, with adequate soil moisture, corn requires a distinctly higher temperature for abundant starch formation and maximum yield.

117. **Organic matter, rate of production.** — A vigorous vine of the Concord or Niagara grape may expose to the light about 10 square meters or more of surface. Careful experiments with other plants indicate that the production (taking no account of respiration) per square meter of surface may be about 1 gram of organic matter per hour,

which has been expressed 1 $g\, m^2\, h$. This gram of sugar involves the use of the carbon dioxid contained in 2.5 cubic meters. At the height of the growing season we may count an average maximum of ten hours of work per day; therefore, a grape-vine of the dimensions indicated has the capacity of $10 \times 10 = 100$ grams per day, equivalent to about 400 grams (about 14 oz.) of fresh substance. To do this all the carbon dioxid would be taken from 250 cubic meters of air.

Looking at this from the standpoint of a crop per acre, an impressive though hazy picture may be had of the atmospheric changes concerned in the making of organic material. A yield of 300 bushels of potatoes on an acre involves, including tops and roots, about 5400 pounds of water-free substance. Estimating as for making fruit sugar (2.5 cu. m. or 3.2 cu. yd. per gram) there would be required all the CO_2 to a height of more than one and one third miles over this acre, assuming no gain meanwhile.

LABORATORY WORK

Chloroplasts. — Study under the microscope the distribution of the chloroplasts in one or more types of leaves available, such as geranium, ivy, and tomato, using hand sections in all cases. Contrast one of the above with the distribution in a species of live-forever, purslane, or Begonia. In the best material study carefully under high power of the microscope the forms of the chlorophyll bodies and their cytological relations. In the young leaves of moss, Elodea, or other convenient material determine how multiplication of these bodies occurs. Study the form of the chlorophyll in desmids, procurable either from an aquarium or any pond containing algæ.

Light and the formation of chlorophyll. — Germinate seed of mustard, radish, or small grain upon moss or in small germi-

nators or pots, placing the vessels in complete darkness. After a few days note the color of the cotyledons and leaves, then place the seedlings in strong diffuse light protected by a bell glass. Observe the greening and note the time required to develop a noticeable green appearance. If convenient, some of the seedlings may be put in a cold room and some at a much higher temperature, conditions of lighting being the same; or in the same room the vessels may be circulated in one case with warm, and in the other case with cold, water. Note the effect of temperature upon the rapidity of greening.

Extraction of chlorophyll. — Make an alcoholic solution of chlorophyll from young leaves of *Vicia faba*, grass, small cereal, or radish. Put the leaves into a flask containing 95 per cent alcohol and heat the flask carefully over a water-bath, the latter being regulated to about the boiling point of alcohol (ethyl alcohol, 95 per cent, boils at about 78° C.). When a fairly strong extract is obtained, pour off the solution into one or more large tubes and protect from the light until used; but fresh solutions should be prepared for each period. Make a careful examination of the solution (1) by reflected light and (2) in diffused or transmitted light. In the examination by reflected light concentrate the rays upon the surface of the solution by means of a hand lens.

Decomposition of chlorophyll in alcoholic solution. — Prepare four small test-tubes (1 inch in diameter) each with about 15 cc. of chlorophyll solution recently boiled and cooled. Place one under each of the following conditions: (1) in direct sunlight; (2) similar to the preceding, but with the solution covered by a thin layer of olive oil; (3) in complete darkness; (4) similar to (2) except in complete darkness. After an hour or two note any change in color; compare the tubes by holding them above white paper, returning each to the same condition as before, and observe after a lapse of about 24 hours.

Separation of the chief pigments of chlorophyll. — Into a test-tube containing about 20 cc. of the fresh chlorophyll solution reduced in alcoholic content to about 80 per cent add also 20 cc. benzole. Note the position taken by the benzole, then shake

vigorously for several minutes, cork, and let stand until the two areas are constant. Describe the separation phenomena.

If a spectroscope is to be employed, as suggested in the next experiment, larger quantities of the materials may be used in the bottle, and a more complete layering effected by the addition of a small amount of water. In that case the two solutions are separated by pipetting or by the burette; each is again washed with the opposite solvent, again separated, and subsequently employed for a determination of the absorption bands of each.

Spectroscopic examination of chlorophyll. — If practicable, make, under standard conditions, a careful spectroscopic examination of a chlorophyll solution of different strengths; also of the constituents dissolved respectively in benzole and alcohol, resulting from the separation of the pigments above. Make a comparison with the living leaf, the latter preferably exhausted of air and injected with water, by being placed in a vessel of water under the exhaust or filter pump.

Evolution of gas during photosynthesis. — Notice that when a mass of alga or aquatic moss, Elodea, or other water-weed is placed in spring water and exposed to the light, bubbles of gas *promptly* accumulate, especially from cut surfaces of the larger plants, and rise to the surface. No such evolution of bubbles takes place with control plants in the dark, although a few bubbles may, of course, gradually form on the walls of vessels or of submersed plants standing for some time exposed to temperature changes.

Quantity and nature of gas released in photosynthesis. — Materials: fresh shoots of a water plant, Elodea or Cabomba; a battery jar, at least 9 × 5 inches, filled with spring water, or with water into which a small amount of CO_2 has been led; a funnel not more than 3 inches in diameter, with short stem; a ½-inch test-tube, preferably graduated, and two pieces of glass tubing of same diameter, — one about 5 inches long, and the other 1 inch; black rubber tubing suitable for attachment to the preceding; 2 pinch-cocks; a ring stand with clamp; and a netted wire basket 3 inches high, with cross rods at the top to support the funnel, all metal being paraffined.

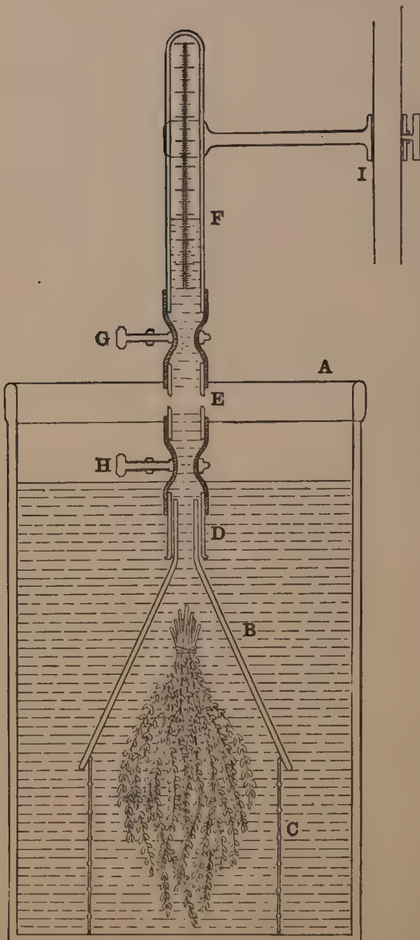

Fig. 58. Apparatus for the determination of oxygen release in photosynthesis.

Set up the experiment about as shown in Figure 58. Arrange netted wire support (*C*), funnel (*B*), and plant in position. (Why so much distance between (*B*) and walls of vessel (*A*)?) The water in the battery jar should more than cover the stem of the funnel. Arrange the series of tubes with rubber connections and pinch-cocks as shown, but fill the series with water and place the finger over (*D*) before inversion over the funnel. Support the series by the clamp. As the bubbles of gas come off they will be caught in (*F*), displacing water. The experiment should be set in fairly bright light until about two inches of water are displaced.

When sufficient gas is caught, note the displacement, or mark accurately with a label. The gas

collected is to be tested as to oxygen content by means of potassium pyrogallate.[1] Unfortunately this solution would also absorb another gas, carbon dioxid, so it is necessary to test first for carbon dioxid. This is accomplished as follows: Clamp pinch-cock (*G*), remove the series of tubes from the support, and pour out water below (*G*), invert and fill (*E*) with a weak solution of potassium hydrate (an absorbent of carbon dioxid) until the liquid rises in (*D*), then clamp (*H*) securely, open (*G*), and shake so that the CO_2 in (*F*) will be absorbed. Fill (*D*) with water, close with a finger, and again open the series under water to liberate any tension from absorption of CO_2. If there is any change in the volume of gas in (*F*), note this, or indicate by a new label. Next, to absorb the oxygen, proceed in the same manner as before, except that fresh potassium pyrogallate is to be substituted for the potassium hydrate solution; also the shaking, in order to absorb all the oxygen, should be continued for several minutes. When the tension is again released by inversion over water, the difference between the preceding and present displacement will show the volume of O_2 caught during the experiment. Compare this with the volume per cent of oxygen in the air. As a check on the accuracy of manipulation, introduce ordinary air into the tube series, and then determine the volume of oxygen. (If graduated tube (*F*) is not available, accurate measurements may be made after the experiment is complete by filling, from a graduated pipette or burette, the tube to the points marked with labels in order to determine the volumes indicated.)

In case the experiment is stopped for any purpose, as on

[1] The potassium pyrogallate solution now strongly recommended by Ganong consists of "1 part pyrogallic acid to 5 parts caustic potash to 30 parts of water." With this quantity of caustic potash 1 gram of the pyrogallate may absorb $\frac{1}{5}$ gram of oxygen; but for uncontrolled experiments it is well to figure at the rate of not less than 1 gram of pyrogallic acid to $\frac{1}{10}$ gram of oxygen. The solution deteriorates rapidly, even in diffuse light, and should be made up immediately preceding its use. It is preferably made by using equal parts of two solutions, each containing one of the constituents in double strength.

account of darkness, but is to be continued later, close pinch-cock (G) and refill with water the (DE) end of the series, before continuing the experiment.

Use of the bubble-counting method to show rate of photosynthesis. — A general idea of the relative rate of photosynthesis under different conditions may be obtained by counting the number of bubbles of oxygen evolved in the same space of time.

a. Method. With a rubber band attach a freshly cut sprig of Elodea or other water plant to a glass rod and submerse in a large test-tube of water at laboratory temperature, or somewhat above 20° C. Water from the tap generally contains sufficient CO_2, but in long-continued experiments it may be necessary to lead in some CO_2 from a generator. Place the tube as above prepared in a wire rack in direct sunlight, and after a few minutes ascertain if the bubbles escape uniformly; also the average number given off in a unit of time, say one minute. If the bubbles do not come off with sufficient uniformity, try another shoot, or seal the cut end of the stem with wax, and then pierce a hole through the latter with a small needle.

b. Light intensity. When a careful count of the bubbles has been made in direct sunlight, remove the tube to light successively weaker; note any change in the rate, and determine where the evolution of gas ceases. If possible, contrast the light intensity at this point with that of the open window, as a standard, using an ordinary photographic actinometer.

c. Temperature. After counting in direct light the number of bubbles given off when employing water at laboratory temperature, transfer the sprig promptly to water brought to a temperature of from 2 to 3° C., but otherwise similar to the preceding. After allowing a few minutes for adjustment, make observation upon the rate of O_2 evolution promptly, before the sunlight has had an opportunity to raise the temperature appreciably; then warm the tube gradually to 20 or 25° C. and note the result.

d. If time permits, determine by the bubble-counting method the rate of photosynthesis under blue and under orange-yellow screens, employing apparatus described in Chapter XVII.

A simple test for starch. — Make a small quantity of a very

weak starch paste (using a piece of starch as large as a lupin seed in 10 cc. of water, and boil a few minutes), then add to this a few drops of an alcoholic solution of iodine and note the intense blue color. This is a common test for starch. Use the iodine test in determining if starch is present in leaves of nasturtium, geranium, or potato, which have been in bright sunlight for a few hours, as suggested in section 112. First extract the chlorophyll by alcohol, then stain with the iodine solution.

Chlorophyll and photosynthesis (starch accumulation). — The necessity of chlorophyll in starch-making may be simply shown by using variegated leaves, white and green, of certain varieties of Coleus, or other greenhouse plants of this nature conveniently obtained. From a plant which has been exposed to sunlight several hours select a leaf, outline the white and green areas, and then test for starch as above suggested. Indicate the relation between the occurrence of starch and the areas outlined. For further proof place the plant in the dark a few hours or over night, so that all starch is removed from the leaves, then replace the plant in light and determine if starch is deposited after a few hours, and in what areas.

Light and photosynthesis (starch accumulation). — The observation that leaves are depleted of starch in the dark is alone sufficient to suggest that no starch has been formed; nevertheless, it is instructive to determine if starch is formed in a darkened and aërated area of a leaf, the remaining portion of which is exposed to light. Employ a Ganong aërated box or light screen (Fig. 57) or simpler devices similar in principle improvised for the purpose. After exposing the leaf for a few hours, apply the starch test and describe the conditions and results.

Obtain two small potted plants, such as Fuchsia, nasturtium, sunflower, or jewel-weed, which shall have been determined to be suitable for starch formation and starch removal in the leaves. Place these in the dark for a few hours or over night, until a test indicates no starch present. Place one in strong light and the other in very weak light, with conditions otherwise as nearly the same as possible. One may be placed under a bell glass and the other under a bell glass covered with manila paper, or with

two or three folds of white cloth. Insert thermometers, and equalize the temperatures as well as possible. At intervals contrast the rate of starch accumulation in the two cases.

Carbon dioxid and photosynthesis (starch accumulation). — In this experiment one plant (*A*) is exposed to a current of air deprived of CO_2, and a control (*B*) to similar conditions, except that the air is natural. Arrange the experiment preferably in the greenhouse or in the open, but a south window is also a possible situation.

Place the plants (Fuchsia is desirable) in the dark over night and keep them darkened until demanded. Each is covered by a tubulated bell glass (and with (*A*) is included a dish of 10 per cent potassium hydrate solution). Seal jar (*A*) to a ground glass or metal base, and cover both with a 2-holed rubber stopper, one hole serving for a connection with an aspirator or filter pump, and the other (in *A* only) connected with potassium hydrate wash bottles. When connections are tight, draw air through (*A*) until a baryta-water wash bottle shows no further CO_2 in the chamber. Then draw through both (*A*) and (*B*) a current of air for several hours, or as long as the experiment may be continued in the light, and test the leaves from each plant for starch.

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TEXTS. *Barnes, Ganong, Jost, Pfeffer.*

CHAPTER X

THE RELATION TO NITROGEN

The significance of the nitrogen content of soils has been recognized deservedly as so important in crop production that a stupendous number of investigations has been directed toward securing the facts regarding the diverse relations of this nutrient. Many of these investigations have yielded data of surprising interest respecting the use of nitrogen by higher plants and by microörganisms as well. Furthermore, the results have been sufficient to demonstrate most clearly the intimate relations existing between soil bacteria and cultivated crops as regards the nitrogen supply. With phosphoric acid and potash it constitutes the trio of nutrients which experience has demanded as usually the most important fertilizers for crop production.

118. Combined nitrogen. — The water-culture experiments (sections 78–80) have demonstrated in a manner sufficiently convincing that the nutrient solutions for higher plants must contain nitrogen. As soon as the supply of this element in the seed is fairly exhausted the addition of combined nitrogen is required. About the middle of the last century Boussingault showed conclusively that the N_2 of the air, unlike the CO_2, is not directly serviceable as a source from which nitrogenous foods

may be made by the green plant. The air contains about 78 per cent of "free" nitrogen, but this vast source is wholly inert naturally except, as later indicated, either through the intermediary of certain microörganisms or by means of electric discharges, whereby this free nitrogen is combined. Nevertheless, since the original rocks seem to contain no nitrogen, the air is the original source of all that at present found in arable soils — constituting often from .1 to .3 per cent of the dry weight of the soil.

119. The nitrogen content of plants. — Nitrogen enters into a variety of organic compounds among which the proteins are of the greatest importance, for these in turn are apparently the main constituents of protoplasm, whether living or dead. Some other compounds, occurring in plants, which contain nitrogen are various amino and amido acids, certain alkaloids, and also nitrates. The protein content is greatest in seeds, storage organs, and meristematic tissues. In beans and other leguminous plants it may amount to 25 per cent of the dry weight, while in wheat straw it constitutes only about 3.5 per cent.

120. Synthesis of nitrogenous bodies. — Animals obtain nitrogen, for the most part, as protein foods, furnished, of course, by the bodies or products of other animals or plants. On the contrary, the rule is that green plants and many fungi and bacteria are able ultimately to construct amido compounds, proteins, and other nitrogenous bodies from certain of the raw materials; that is, from some of the mineral nutrients and photosynthates (carbohydrates).

Proteins represent an immense group of compounds (sections 147–148) with a relatively enormous molecule.

They must contain carbon, hydrogen, oxygen, and nitrogen; many contain sulfur, certain forms phosphorus, and others apparently mineral bases, the latter either combined or as ash. Proteins may be regarded as perfect foods for protoplasm.

Lack of knowledge respecting the proteins renders impossible a clear picture of their synthesis, although much may be inferred from the decomposition products, which have been extensively studied. Speaking generally, the amides (containing the group NH_2) seem to represent products intermediate between certain of the raw materials (organic acids or carbohydrates and nitrates) and the proteins. Glycin, for a simple example, is an amido-acetic acid [$CH_2(NH_2) \cdot COOH$] in which the amide group replaces one H of the acid. It may be assumed that protein is constructed from amido compounds, especially from those derived from carbohydrates, some of which may be further modified by the incorporation of sulfur from sulfates, and others by the introduction of phosphorus from phosphates.

121. Soil nitrogen. — Some data regarding the nitrogen relations of higher plants have been exhibited in connection with the discussion of mineral nutrients. On account of the unusual importance of the nitrogen supply in any permanent system of agriculture, special attention should be given to the interesting transformations of nitrogenous materials in the soil, and likewise the building up of nitrogenous bodies within the plant require some consideration.

It is now a matter of common knowledge that nitrogen exists in the ordinary arable soils in a variety of com-

binations. Aside from the N_2 of the air there may be undecomposed organic matter, containing most of the compounds of the plants and animals which it represents. There is also the converted organic matter, that resulting from decay, — commonly designated humus, — which may consist, in fact, of a variety of substances. Finally there is the inorganic nitrogen, including nitrates, often a small proportion of nitrites, and compounds of ammonia. The total nitrogen content of the soil is therefore most diverse, but in productive agricultural soils there is invariably a considerable nitrate content during the growing season.

It is probable that under exceptional conditions higher plants may use to a certain extent organic nitrogen in the form of amido compounds, but, practically speaking, it seems certain that such organic bodies are not absorbed or utilized in sufficient quantity to make this question one of importance.

122. Nitrites. — The nitrites are commonly injurious, and the presence of these in any quantity is a sure indication of unfavorable conditions. As will be shown subsequently, they occur as temporary products during the oxidation of ammonia to nitrates, but may be looked upon under favorable conditions as merely transitory.

123. Nitrates. — By means of water cultures it is relatively a simple matter to determine that nitrates are the most favorable source of nitrogen in water or sand cultures under normal conditions, and more especially under sterile conditions. It is certain that such compounds are usually absorbed by the plant unchanged. Nitrates of the various nontoxic bases are therefore valuable direct fertilizers, and the data furnished by the

extensive fertility experiments throughout the world lead to the conclusion that the maintenance of an adequate nitrate supply in the soil, or of conditions leading to the transformation of nitrogenous matter into nitrates, is an important principle in production.

The nitrates are readily soluble, and while this character enhances the rapid action of such substances as fertilizers, it is at the same time a quality making possible constant loss through percolation and leaching. It is evident, therefore, that unless the nitrate supply is maintained by natural or artificial means, exhaustion of this requisite element would sooner or later occur. Fortunately, there are both natural means as well as conditions of cropping which may suffice to maintain and to increase the nitrogen content, as developed later.

124. Compounds of ammonium. — Prior to the latter quarter of the last century the prevailing view was to the

FIG. 59. Fertilization of grass land, all plats given muriate of potash and acid phosphate; also, from left to right, no nitrogen, ½ nitrogen ration, and full nitrogen ration. [Photograph from the Rhode Island Exp. Sta.]

effect that compounds of ammonium (such as the sulfate, chlorid, and nitrate) should be considered the important sources of nitrogen for plants, and the weight of Liebeg's opinion was upon it. At that time the cycle of changes involving nitrogen was incompletely known. Unques-

tionably the addition of ammonium salts to the soil gave increased yields, and the inference was that they were directly beneficial; that is, that they were absorbed as salts of ammonium.

Subsequently, when it was determined that, as a result of nitrification, ammonium compounds may be oxidized, ultimately to nitrates, the dominant view was to regard nitrates as practically the only source of nitrogen for crops. This is still held by many, but the relatively recent experiments of Mazé,[1] Hutchinson and Miller,[2] and others seem to indicate that salts of ammonium are directly absorbed. In some cases nitrogen in the latter form afforded growth equal to that where nitrates were employed, and the nitrogen content of peas is reported greater when ammonia is the source of nitrogen. Nevertheless, the salts of ammonium are more toxic than nitrates, this toxicity exhibiting itself at the lower concentrations merely in depressing the growth of roots.

125. The sources of soil nitrates and ammonia. — Briefly stated, the supply of nitrates and ammonium compounds in the soil annually removed by crops, by leaching, and through denitrification (section 130) are or may be renewed by the following means, most of which are subsequently discussed: —

(1) By the decomposition or decay of organic matter, accomplished by microörganisms.

(2) By means of the bacteria producing and inhabiting the root-tubercles of leguminous plants, which bacteria possess the power to "fix" atmospheric nitrogen.

[1] Mazé, P., Ann. de l'inst. Pasteur, **14**: 23–45, 1898.

[2] Hutchinson, H. B., and Miller, N. H. J., Journ. Agl. Sci., **3**: 179–194, 1909.

(3) By the action of certain soil bacteria and fungi which are also able to utilize atmospheric nitrogen.

(4) By the ammonia returned to the soil as a result of rainfall; but since this, in general, is that which escapes from the soil into the air, it is negligible.

(5) As a result of electrical discharges nitrous and nitric acids may be produced in the air and through rains brought to the soil, but this amount is relatively inconsiderable, consisting, under the most favorable conditions (in the moist tropics), of about five pounds per acre annually.

126. Ammonification. — The remains of plants and animals are "returned" to the soil through processes of decay and putrefaction brought about largely by means of fungi and bacteria. Decay is a relative term usually implying decomposition without the production of malodorous compounds, and commonly taking place with access of oxygen. In putrefaction ill-smelling compounds result, usually from the decomposition of nitrogenous substances, taking place, as a rule, with poor oxygenation.

A result of both of the above processes is that nitrogenous compounds are broken down into ammonia, carbon dioxid, and other products. This reduction to ammonia constitutes what is known as ammonification. Under favorable conditions a large part of the ammonia is held in the soil by entering into combinations with the soil bases. During this decomposition many substances more or less injurious may be at least temporarily set free in the soil.

Numerous species of bacteria and fungi affect decomposition. Bacteria are particularly important in arable soils, especially such species as *Bacillus mycoides* and *B.*

vulgaris, while many common molds, punks, and mushrooms are among the various fungi inducing decay in the forest.

127. Nitrification. — Ammonification is the completion of the first stage in the cycle of changes whereby nitrogenous matter may be converted to nitrates, the succeeding transformations being as follows: —

(1) Oxidation of the salts of ammonium into nitrites.

(2) Oxidation of nitrites into nitrates.

The production of nitrates (ultimately) from organic matter has been long known and practically carried out by means of the niter beds so much employed a generation or two ago. A process wholly similar in nature has given rise to the natural deposits of niter and is constantly at work in the best arable soils to develop nitrates.

128. Nitrifying organisms. — In 1877 it was first determined (Schloesing and Müntz) that nitrification is effected by bacterial agencies, and Winogradski, Warington, Godlewski, and others have laid bare many important features affecting the action of the organisms involved. These bacteria are widely distributed in soils and in drainage or run-off waters.

The organisms oxidizing ammonia to nitrites (nitrite organisms) are small, oval, motile cells generally included in the genus Nitrosomonas, while those oxidizing nitrites (nitrate organisms) are considered nonmotile and included in the genus Nitrobacter.

These two types of bacteria are commonly associated in the soil, and all forms seem to exhibit the peculiar physiological quality of being able to make their own carbohydrate food from CO_2 and water. Unlike green

plants, they accomplish this in the absence of light (chemosynthetically).

In cultivated soils they are most abundant below the surface mulch, and down to the limits of frequent culture. The following table shows the distribution of nitrifying bacteria and nitrates at different depths in a Dakota soil[1]: —

Soil Depth	Colonies of nitrifying Bacteria	Nitrates, Pounds per Acre
3 in.	2300	415.9
6 in.	2300	415.9
12 in.	600	234.3
18 in.	200	196.6
24 in.	10	430.9
36 in.	0	674.9
48 in.	0	316.3
60 in.	0	395.3
72 in.	0	247.0
84 in.	0	293.9

129. Conditions favoring nitrification. — The general conditions favorable for nitrification in soils are good aëration (oxygen and carbon dioxid), a medium water-content, a soil temperature not to exceed 40° C., the presence of a basic compound such as calcium carbonate, and the absence of much soluble organic matter and free ammonia. In general these conditions are those of good sanitation and tilth, a judicious application of lime, and such a rotation of crops as will produce and maintain the best of soil conditions. The advantage of paying the

[1] Ladd, E. F., North Dakota Agl. Exp. Sta., Bul. **47**: pp. 685–704.

closest attention to those conditions resulting in the highest nitrification is obvious.

As a rule nitrate formation in the soil begins rapidly in the spring and with most crops a maximum is reached during the first half of the growing season; subsequently there is a fall in the nitrate content which may approach a minimum in the late fall, or with the maturity of the crop. Recent studies upon the relation of crops to the nitrate content have developed a number of interesting views which, however, may not be discussed in this place.

130. Denitrification. — Almost the counterpart of nitrification is the process exhibited by many micro-organisms of reducing nitrates and nitrites, known as denitrification. From an agricultural standpoint the most serious case is that of the reduction of nitrates and nitrites with the formation of free nitrogen, and the consequent loss to the soil of combined nitrogen. In many cases, however, the reduction is not carried so far as to form free nitrogen.

A large number of organisms are able to accomplish nitrate reduction, both bacteria and fungi; but the conditions under which denitrification occurs are not usually those developed under the best agricultural practices.

Aside from the presence of necessary nitrates this reduction requires the presence of considerable soluble organic matter and poor aëration. Many of the organisms which induce denitrification are aërobic forms which in the presence of sufficient oxygen show no tendency toward nitrate reduction. It is apparent that saturation of the soil with water after heavy manuring may actually result in nitrogen loss and frequently also in the production of injurious compounds in the soil.

131. Nitrogen fixation. — Since by nitrification (including ammonification) nitrogenous bodies are merely transformed into inorganic nitrogen, this does not increase the total nitrogen of the soil. Moreover, the nitrogen brought to the soil as a result of electrical discharges is a small amount. It is then apparent that the loss of combined nitrogen over the surface of the earth through the washing away of sewage, the leaching of soils, and the liberation of free nitrogen in denitrification would mean in time a nitrogen famine. There is, however, a more than compensating process of nitrogen fixation.

132. Organisms which fix free nitrogen. — Since the classical researches of Hellriegel and Wilfarth, there has accumulated a vast array of facts and observations with respect to the fixation of free nitrogen by micro-organisms.[1] The rôle played by the bacteria of the leguminous tubercles was the first to be clearly demonstrated, but the importance of certain saprophytic soil bacteria in the process of nitrogen accumulation was fully recognized a short time later. Strikingly little has been said in agricultural publications regarding the rôle which may be played by fungi in this process. Nevertheless, as a result of a series of observations and experiments, it is now commonly held that certain fungi are likewise important in fixation, and this view is regarded in the succeeding discussion, although there is some doubt respecting the real importance of the fungi in this connection.

133. Bacteria of leguminous tubercles. — In recent

[1] The evidence now commonly accepted is to the effect that certain bacteria and fungi alone among all organisms possess the capacity for nitrogen fixation.

FIG. 60. Roots of vetch with clusters of fan-shaped tubercles.

times no plant structures have, perhaps, attracted more attention than the nodules, or tubercles, of the leguminous

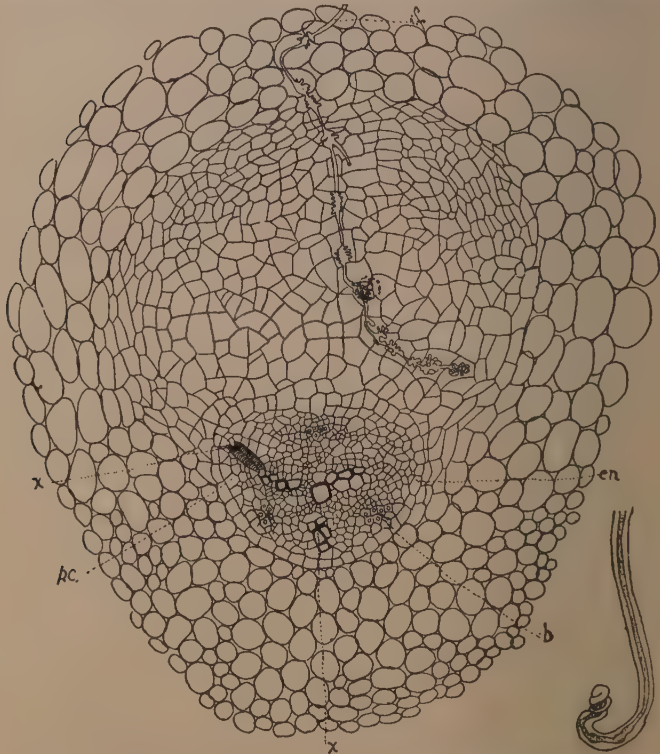

Fig. 61. Infection thread and abnormal tissue in a tubercle developing upon the root of *Vicia sativa*. At the right, infection thread in root-hair. [After Geo. F. Atkinson.]

plants. These structures are abnormal growths resulting from the attacks of parasitic bacteria, Figures 60 and 61.

Parasites generally make little or no return to the hosts in which or upon which they live. These nodule bacteria, *Pseudomonas radicicola*, are exceptions to this rule. The tubercles are, in fact, root colonies of the micro-organisms. The bacteria get their carbon, minerals, and water from the host, yet ultimately they give to the host in return combined nitrogen which has been acquired by the fixation of the free nitrogen of the air.

In the earliest days of historic agriculture, it was known that leguminous plants benefit the land for succeeding crops. The methods by which benefit results were, of course, unknown. When it was ascertained that the chief benefit is concerned with the accumulation of nitrogen, it was assumed that these legumes and other plants might themselves be able to assimilate atmospheric nitrogen. Boussingault's experiments clearly demonstrated the incorrectness of this view. His work was convincing, and finally attention was directed to the tubercles of leguminous plants as the cause of nitrogen accumulation.

Hellriegel and Wilfarth demonstrated that on sterile soil no tubercles are present and no nitrogen is fixed. The complete chemical and biological studies which subsequently followed have led to a full confirmation of the work of Hellriegel and his associate. It is now a simple matter to determine that leguminous plants growing in the absence of the bacteria are wholly dependent upon the soil supply of combined nitrogen, whereas, in the presence of the proper bacteria, such plants are able to reach normal development with a deficient soil supply of nitrogen, and even to give to such deficient soil, through root decay, an increased nitrogen content.

The bacteria producing the tubercles seem to have acquired at least racial specialization, so that no one form of the organism will infect all leguminous plants. The introduction of a particular legume into a region in which that plant (or a closely related species) has not been grown may necessitate, for best results, "inoculation" of the soil or of the seed employed.

FIG. 62. Bacterioids from legume tubercles: *Melilotus alba* (*1*), *Medicago sativa* (*2*, *3*, and *5*), and *Vicia villosa* (*4*). [After Harrison and Barlow.]

Formerly the organism was introduced by importing soil from a locality in which the legumes had been grown. This method has many disadvantages, and at the present time a very thorough test is being made of the practicability of employing pure cultures of the organism desired. Good results have been secured with pure cultures in many cases, but in some particulars the method is still in the experimental stage.

134. Certain saprophytic soil bacteria. — Evidence that saprophytic soil bacteria are able to fix free nitrogen was afforded when Berthelot found in 1885 that bare soil with its normal population of micro-organisms may considerably increase in nitrogen content over and above that added through rainfall. At the same time, no increase occurred upon eliminating micro-organisms by steaming.

Fig. 63. Crimson clover inoculated (background) and uninoculated (foreground). [Photograph by J. F. Duggar.]

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Ten years later Winogradski isolated *Clostridium Pasteurianum*, an organism which proved to be capable of fixing free nitrogen when grown in the absence of air (oxygen), also similarly capacitated in the presence of air when associated with other bacteria utilizing free oxygen. Since that time much work has been done. Several other species of soil bacteria having the power of fixation have been isolated, these latter being included under the genus Azotobacter. They are common and important in arable soils containing a relatively small amount of combined nitrogen; moreover, their activity is enhanced by the presence of considerable lime and by general fertility as regards the other mineral nutrients. From the majority of experiments thus far reported it does not appear that the addition to the soil of cultures of these organisms has occasioned increased nitrogen fixation.

135. Fungi. — The investigation of nitrogen fixation by fungi has yielded many data of interest, although there is some conflicting evidence. Fixation of nitrogen by fungi was reported as early as 1862, but the more important work has been done since 1895. Among several saprophytic and parasitic species employed, Saida secured maximum fixation with cultures of *Phoma Betæ*, a fungus normally parasitic upon sugar-beets.

Several observers have reported fixation for a few of the common molds of soils and decaying vegetation, including *Aspergillus niger* and *Penicillium glaucum*. In all cases the organisms were grown in pure cultures, either in the absence of combined nitrogen, or in the presence of very small quantities of such compounds. In no case does the amount of nitrogen fixed amount to more than a few milligrams.

136. Mycorhizal fungi. — Ternetz has isolated and tested a fungus from the roots of certain heaths. The association of root and fungus is known as mycorhiza. This fungus proved to be a species of Phoma, and several strains of it were found to show a high capacity for nitrogen fixation. In fact, while the total amount of nitrogen fixed in a given period of time is relatively small, the fixa-

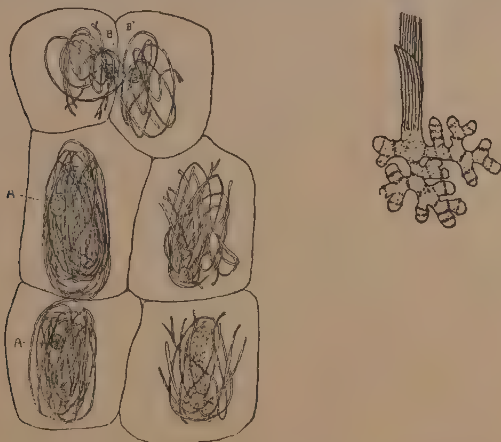

Fig. 64. Mycorhiza of the orchid Corallorhiza, also cells showing the hyphæ. [After M. B. Thomas.]

tion per gram of dextrose used by the fungus indicates that in pure cultures fixation is more economic than with any other organisms yet investigated. The following table affords a comparison of the efficiency of several strains of this fungus as compared with certain soil bacteria : —

The Phoma discussed above develops an endophytic mycorhiza, penetrating the cells. This endophytic form

Organism	Time in Days	Dextrose furnished, grams	Nitrogen Fixation, milligrams	Nitrogen Fix. per Gram Dextrose, milligrams
Clostridium Pasteurianum . .	20	40	53.6	1.34
Clostridium Pasteurianum . .	20	20	24.4	1.22
Clostridium Americanum . .	30	1.25	4.6	3.7
Clostridium Americanum . .	30	5	8.2	3.01
Azotobacter chroöcoccum . .	35	5	42.7	8.56
Azotobacter chroöcoccum . .	35	12	127.9	10.66
Phoma radicis Oxycocci . .	28	7	15.3	18.08
Phoma radicis Andromedæ .	28	7	7.3	10.92
Phoma radicis Vaccinii . .	28	7	15.7	22.41

of mycorhiza occurs also in several orchids and in a few other plants. Many common forest trees, such as beech and pine, likewise exhibit mycorhiza. In the latter case the fungus invests the root with a mycelial weft, the threads merely coming in close contact with the cells (ectophytic). These fungi are believed to be not only of importance to the tree as absorbing organs for water and nutrient salts, but possibly in the fixation of nitrogen. Nevertheless, this point has not been established.

137. General sources of supply of nitrogen. — From the data presented it is apparent that the nitrogen problem in plant production is one of peculiar interest and diversity. Commercial sources of nitrogen for plant production may be natural supplies of nitrates, compounds of ammonium (chiefly the sulfate, as a by-product of coke and gas making), waste and prepared animal products, and green-manure crops (especially legumes). In addition, good conditions for fixation by bacteria and fungi and

rotation with legumes are supplementary means of nitrogen restoration. Finally, electric fixation is a source of supply.

138. Electric fixation of nitrogen. — In recent years several methods have been devised for the oxidation of atmospheric nitrogen. These methods involve the use of cheap power, since high-power electric currents are necessary. Those which are now important in the production of materials commercially valuable as fertilizers require also a cheap source of lime. The two methods referred to are known respectively as the Birkeland-Eyde process and the calcium carbide process. By the former a basic lime nitrate is produced, and by the latter a lime-nitrogen consisting of calcium cyanamid and calcium cyanide. The first mentioned product, which is much employed in northern Germany, is a direct fertilizer, whereas the latter must first undergo decomposition in the soil. The cyanamid is more easily handled. the basic nitrate being strongly hydroscopic.

LABORATORY WORK

Ammonification.[1] — The decomposition of protein with formation of ammonia may be demonstrated by the action of certain bacteria upon egg albumen. Prepare a solution containing about 2 grams of egg albumen in 50 cc. of water, and to prevent coagulation add 50 cc. of .05 ferrous sulfate. Pour about 10 cc. of the solution into each of several test-tubes, sterilize for 1 hour at 100° C., cool, and inoculate some of these with a pure culture of *Bacillus mycoides*, or some other organism reported to possess

[1] For more experiments upon ammonification, nitrification, and related phenomena the student should consult especially Percival's "Agricultural Bacteriology," 1910.

the power of ammonification. Place the cultures at a temperature of 28 to 30° C., and in two weeks test the inoculated and uninoculated tubes for ammonia with Nessler's solution.

The Nessler solution is prepared by dissolving 2 grams of potassium iodide in 5 cc. of hot water, while warm add mercuric iodide to excess of solution, cool, dilute with water to 25 cc., shake, settle, filter, and then dilute the filtrate to 50 cc. with a concentrated solution of caustic potash. This solution assumes a yellow color when there is added to it a few drops of a solution containing ammonia.

Nitrification. — A crude but simple demonstration of nitrification phenomena, usually successfully carried out, may be made with impure cultures as follows: —

Prepare a solution containing —

Ammonium sulfate	.5 gram
Dipotassium phosphate	.5 gram
Sodium chlorid	.2 gram
Magnesium sulfate	.2 gram
Ferrous sulfate	.05 gram
Water	200 cc.

Weigh out .5 gram of basic magnesium carbonate into each of four small Erlenmeyer flasks, add to each 50 cc. of the above salt solution, plug with cotton, and sterilize. When cool inoculate three of the flasks with a small quantity (about .1 gram) of garden loam taken 5 or 6 inches below the surface of the soil. Save the fourth flask as a control. Place all at a temperature of 28 to 30° C. Once a week remove from the inoculated flasks from 3 to 5 cc. of solution and make the following tests: —

1. For ammonia. Employ Nessler's solution.

2. For nitrites. Acidulate with sulfuric acid about 2 cc. of the solution, add a few drops of potassium iodide and starch paste. If nitrates are present the starch is colored blue from the reduced iodine.

3. For nitrates. When from (2) it is evident that nitrites are no longer present, dissolve a crystal of diphenylamine in about 1 cc. of sulfuric acid in an evaporating dish. The addi-

tion of a drop or two of the culture solution will give in the presence of nitrates (no nitrites being present to give the same reaction) a blue-violet color. At the close of the experiment test thoroughly the control in order to determine if the ammonium salt has remained unchanged.

Denitrification. — To about 100 cc. of prepared nutrient bouillon (consult any bacteriology) add 3 grams of sodium nitrate, and pour about 10 cc. of the solution into each of several test-tubes. Inoculate the tubes from a pure culture of some denitrifying organism, such as *Bacillus denitrificans*, or each tube with about .5 gram of fresh cow manure. Place the tubes at a temperature of from 30 to 35° C. Note all the changes in appearance of the culture and test occasionally for nitrates as in the preceding experiment. Discuss the results.

Root tubercles. — Study the root tubercles of several leguminous plants, such as vetch, red clover, and alfalfa, with special reference to the form and distribution of the nodules.

Examine prepared slides to determine the distribution of the organism within the tissues. If prepared slides are not at hand, make sections, stain in gentian violet, counterstain with orange G., locate the band-like colonies of the organism, and note the general conditions of the tissue modifications.

Crush a bit of tissue from the inner portion of the nodule on a clean cover glass, dry, and stain several hours in dilute gentian violet; then rinse the cover glass, dry, and mount in balsam. This affords a satisfactory preparation for an examination of the organism (Fig. 62).

If facilities are at hand, determine the necessity of the bacteria for tubercle production and contrast the growth of certain legumes in inoculated and uninoculated soil. The experiment can only be relative unless much care is taken with sterilization precautions. The materials needed are six pots of fairly poor soil, a pure culture of the root tubercle bacteria, seed of the legume host plant, and a .2 per cent solution of formaldehyde. Steam the pots of soil 2 hours, disinfect the seed by soaking 1 hour in the formaldehyde solution, then sow a few seed in each pot. Inoculate three of the pots with the pure culture and leave three

as controls. Place the pots in the greenhouse upon fresh cinders, separating the two lots and protecting the pots as well as practicable from contamination by dust or soil from other pots or beds. Water with distilled water only. After the plants have grown sufficiently, compare the two lots, as indicated, for nodule formation and amount of growth.

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TEXTS. *Barnes, Jost, MacDougal, Pfeffer, Peirce.*

CHAPTER XI

PRODUCTS OF METABOLISM; DIGESTION AND TRANSLOCATION

FROM the discussion of the general relations of the green plant to carbon and nitrogen it has been developed that a variety of organic products are characteristic of the plant cell and plant body. Beginning, in the typical case, with those which may be regarded as the products of photosynthesis (photosynthates), on the one hand, and with the elementary organic substances containing nitrogen, on the other, there may be built up in various ways diverse series of organic compounds, constituting the plant body and including, of course, the protoplasm and the cell walls. This shall not be taken, however, to indicate that there is a normal sequence of products, or a continuous building up, for, as will be shown subsequently, the building up may be interrupted at any point and breaking down may occur. The food products are then utilized in a manner dependent upon the specific nature of the substances and upon the chemical requirements of the cell. Pfeffer has distinguished plastic and aplastic substances. The former term is used by him to include substances which may be used as food, which may be mobilized and utilized in metabolism; while aplastic substances include the solid and permanent constituents of the cell, — such as the cell wall, — and certain by-products or waste ma-

terials. It is difficult, of course, to draw any line between these two types of substances.

139. Metabolism. — All of those chemical changes which take place within the body incident to growth and development are commonly included under the term "metabolism." These changes may be constructive (or anabolic) and destructive (or catabolic). Some brief indications have been given respecting the building up of a few of the more important organic compounds, and it is necessary to include now a somewhat comprehensive view of the general relations of a few of the foods and by-products and some characteristics of these materials.

140. Temporary foods, storage products, and permanent structures. — It would seem that many substances produced within the cell are temporary, that is, they may be labile compounds readily used in the metabolism of the active cell. If formaldehyde is a first product of photosynthesis, it is necessarily one of this nature. Naturally the transient compounds are the lesser known as plant constituents; but it seems certain that many simple carbohydrates, fatty acids, amides, and the like are distinctly temporary. Nevertheless, a substance which is temporary in one plant may be accumulated in another.

Whenever the food manufactured is in excess of that used, it accumulates, and may be regarded as a storage product. The chlorenchyma of higher plants is a temporary storage structure, for starch or other substances may accumulate in the cells of this tissue during photosynthesis. Specialized storage structures are extremely common among higher plants, and to such organs the food in diffusible form is transported.

It has been noted that certain mineral constituents migrate from old organs to the seed. In an analogous manner organic products are accumulated. Storage may also occur in bulbs, tubers, or aërial stems, roots, leaves, and fruits. It is, of course, such natural storage organs that have been seized upon particularly as food for man and feeding stuffs for animals, and many of the plants possessing these have been wonderfully improved through selection and breeding.

A storage organ of available food-material has a phylogenetic reason for existence in the fact that it has to do with subsequent growth and fruiting or with the propagation of the species. Seeds, bulbs, tubers, and other such structures are essentially propagative devices, and it is not uncommon to find that they possess the capacity to lie dormant for a period, or to withstand desiccation.

141. Annuals, biennials, and perennials. — These terms are used to imply one or more seasons of growth. When an annual plant, like the oat, reaches maturity by gradual, natural means, a very large part of the mobilizable carbohydrate and protein material is deposited or accumulated in the fruit or seed. The work of the plant as a whole is done, and there is no great wastefulness of readily used substance in the dead tissues. In the case of a biennial plant, such as the sugar-beet, which has grown for one season, the leaves have died, but the root has become an organ for a great accumulation of sugar and other food-materials. The next season by virtue of this stored food the energies of the plant may be vigorously directed toward the production and maturity of seed.

The potato uses up during the early part of the season

not only the starch of the "seed tuber," but also practically all of the starch which is made daily by the leaves, in the production of stem and leaf structures — additional starch-making surfaces. The growth of new tubers develops slowly at first, but finally the energy of leafy shoot "vegetation" wanes, and then a considerable surplus of carbohydrate is accumulated as starch in the tubers. In consequence, at maturity about 80 per cent of the dry matter of the tuber is starch.

When a tree ceases to make food-material in the fall, there may be little or there may be much starch already accumulated. A peach tree, for example, heavily laden with young fruit in July may make each day a considerable quantity of starch. The latter may be found by the usual test applied to the leaves. The starch, however, is in considerable part used every day to furnish the carbohydrate used in the building of wood, in the making of fruit, and ultimately in respiration, so that only when the fruit is becoming ripe and the development of new wood is checked may there be a surplus of starch to accumulate in trunk and branches. After the ripening of the fruit much more starch may be made and accumulated in the twigs as a reserve for the young growth of another season. Such accumulations of food-material are indispensable, for in the peach thousands of blossoms are produced and the fruit set before the leaves are unfolded, a result of using food-materials that represent the work of the previous season.

Many varieties of apple do not ripen until after the leaves fall, and it is possible that this holding and sustaining of the fruit so long (meanwhile using stored food-

material) may be a factor in the apparent tendency toward biennial fruit production, that is, to a greater production in alternate years. It stands to reason that a too heavy yield of fruit one season may have some effect upon the crop of the next year, although this tendency may be offset to a considerable extent by good culture, fertilization, and favorable season.

142. Carbohydrates. — The carbohydrates include the sugars, starch, cellulose, and many of the other compounds containing carbon, hydrogen, and oxygen. They constitute the bulk of food-materials in general. In these substances the molecule contains hydrogen and oxygen in the proportion of 2 : 1, or as in water; and the number of carbon atoms is usually six or a multiple of six, but in some compounds five. The following are some important classes of these compounds: —

(1) Monosaccharids (sugars), $C_6H_{12}O_6$, including glucose, fructose, and galactose.

(2) Disaccharids (sugars), $C_{12}H_{22}O_{11}$, including sucrose (cane sugar), lactose (milk sugar), and maltose.

(3) Polysaccharids or amyloses, $n\ (C_6H_{10}O_5)$, including such compounds as starch, inulin, dextrin, glycogen, and cellulose.

Briefly stated, the disaccharids and polysaccharids are for the most part readily convertible into monosaccharids through hydrolysis. This may be accomplished by boiling with acids, and also through the action of certain other compounds of metabolism, the enzymes, subsequently discussed. The transformation of cane-sugar may be represented as follows: —

$$C_{12}H_{22}O_{11} + H_2O = C_6H_{12}O_6 + C_6H_{12}O_6,$$

that is, producing dextrose and levulose. The hydrolysis of the polysaccharids may involve a series of changes in which water is taken up and ultimately *n* molecules of hexose sugar (or sugars) are split off.

143. Sugars. — The commoner forms of sugar found in plants are sucrose (cane-sugar), glucose (dextrose), and fructose (levulose). Glucose and fructose are apparently important products in the metabolism of cells usually, but these compounds are often promptly used in general metabolism, especially in the building up of other products. There may be no accumulation of them in the plants where they are being constantly manufactured. Accumulation does occur, however, particularly in ripening fruits, such as the grape, peach, prune, and date. In the raisin the characteristic brown nodules of this sugar may be seen. Indirectly these sugars are of much commercial value, for sweetness and flavor together determine the prices paid for fruits, prices which are in general far above their actual food value.

The monosaccharids are reducing sugars, precipitating heavy metals from solutions of their salts upon heating. Maltose also possesses this quality, but cane-sugar does not. A standard test for reducing sugars is obtained by Fehling's solution (see Laboratory work), consisting of copper sulfate in an alkaline solution of potassium sodium tartrate. Upon boiling with this solution a brick red precipitate of cuprous oxide is produced.

Sucrose is the form in which sugar commonly accumulates in plant cells. From the stems of the sugar cane and from the root of the sugar-beet there were extracted during 1909 nearly 15,000,000 tons of commercial sugar. The

juices of selected races and strains of the two plants indicated may contain from 14 to 18 per cent of sugar, and the history of the breeding of the highly productive races of the sugar-beet is of special physiological interest. Sorghum and a few species of tropical palms also contain cane-sugar in sufficient quantity to be of commercial importance. Sugar maple (*Acer saccharum*) growing in northern latitudes yields a sap which in the usual time of cupping (late winter or early spring) may contain from 2 to 5 per cent of cane-sugar, besides other substances imparting the peculiar flavor for which this sugar is prized.

144. Starches. — The great majority of green plants produce starch (Fig. 65). There are some exceptions among several orders of flowering plants, especially certain monocotyledons (Sect. 112); and certain groups of algæ do not possess this capacity, notably the families of blue-greens and browns.

The starch molecule is very complex and difficult of exact study, but the occurrence and reaction of the starches are well known. Starch occurs in the form of insoluble grains with a characteristic general appearance, varying considerably, however, in form, size, and markings in the different plants in which produced. The grains may be simple, semicompound, or compound. Very large grains, often so large as to be visible to the unaided eye, are found in the root-stock of Canna; those of potato are of medium size; in rice the components of the compound grains are small and numerous; while in spinach they may be extremely minute, and according to Nägeli as many as 30,000 may be united together.

Starch grains are produced within plastids, — chloro-

plasts and amyloplasts (leucoplasts), — and the exact method of formation is imperfectly understood. It is a general belief that starch is formed from glucose[1] and under the influence of one or more enzymes. The latter are believed to be active in starch production, as a rule, when carbohydrates exist in the cell in considerable excess of use.

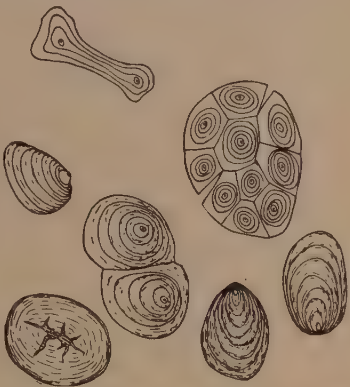

FIG. 65. Starch grains of various forms.

Schimper considers the starch grain to be a spherite made up of a multitude of needle-like crystals radiating from the center. The striated appearance commonly exhibited seems to be due to difference in nutrition during the formation, and the eccentric arrangement of the morphological center may be due to the development of the grain near the periphery of the plastid.

Starchy products constitute a very large portion of the food of man and of domestic animals, so that many products are valuable chiefly from the high starch content. In passing from colder to warmer regions some of the more important starch-producing plants are the following: the small cereals, buckwheat, corn, beans, potatoes, sweet potatoes and yams, cassava, rice, yautia, arrow-root,

[1] The view is also current that the starch molecule is split off from protein material of the plastid.

sago, tapioca, bread-fruit, banana, and many other vegetables and fruits. Reckoned in per cent of dry weight, the potato tuber contains a starch content of about 80 per cent, while corn and many cereals may contain 60 per cent or more. According to König starch contains on the average about 15 per cent water, 1 per cent nitrogenous bodies, and generally much less than 1 per cent of ash.

Upon hydrolysis starch yields, as subsequently shown, first dextrins, then maltose, and this is ultimately transformed to glucose, although some of the dextrin (about one fifth) is more resistant to hydrolysis.

Inulin, an amylase less complex than starch, is characteristic of the tuberous roots of Dahlia and of some other composites, although occurring also in other plants. It is dissolved in the cell-sap, but may be crystallized out as spherites. These crystals are soluble in hot water. It yields fructose on hydrolysis.

145. Cellulose. — The cell-walls consist in large part of a substance which passes under the general name of cellulose $n(C_6H_{10}O_5)$. Cell-walls are frequently impregnated with gummy, metallic, or other substances; this is the usual case with epidermis, cork, wood, and the like. Nevertheless, some form of cellulose forms a large per cent of the walls of flowering plants.

The celluloses proper resist hydrolysis with weak acids, and except at the time the cell-walls are being laid down they are unimportant in metabolism. Hemicelluloses are forms which are readily hydrolyzed, yielding monosaccharids other than glucose. They constitute, in fact, the reserve cellulose deposited upon the cell-walls in the endosperm of many seed and some other storage organs,

especially in the seeds of palms. This reserve food becomes available during germination.

146. Fats and oils. — Fats and oils are far more common and important constituents of plants than is popularly supposed. In Liliaceæ and a few other monocotyledonous orders oils replace starch as the first visible photosynthetic product. Oily bodies occur in active cells often as small droplets in the cytoplasm. In a variety of seeds the amount of fatty substances is considerable, a part occurring as globules or as crystals.

Among the more important fats and oils may be mentioned those from corn, coconut, various palms, olives, mustard, poppies, flax, castor-bean, Bergamot-orange, carnation, Brazil-nut, cotton, etc. Thousands of tons of palm and coconut oil are annually imported into Europe and constitute an important item of trade. The value of the cotton-seed oil produced during 1909 and 1910 is estimated to have been upwards of $300,000,000.

Oils and fats may be identified by comparatively simple tests and they are obtained for commercial purposes by crushing and pressing, or by extraction.

147. Proteins. — The vegetable proteins are numerous, and they vary greatly in physical and chemical characteristics. They may occur in solution in the cell vacuoles, partially dissolved in intimate association with the protoplasm, and as solid forms — crystals or granules. The latter occur especially in storage organs or tissues with reduced water-content, usually associated with carbohydrate storage products, oil, and other substances, as in many legumes.

The vegetable proteins have been studied more particu-

larly in the seed, so that the storage forms are better known. The aleurone grains of the endosperm of cereals are familiar protein bodies, and in this case they are found abundantly in the outer layer of the endosperm, while starch is more abundant within.

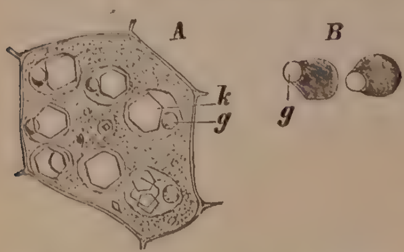

FIG. 66. Endosperm cell (*A*) of Ricinus in water; aleurone grains (*B*) in olive oil; protein crystal (*k*) and globoids (*g*). [After Strasburger.]

The gluten of wheat consists of a variable mixture of proteins. Flour may contain about 10 per cent of this material and about 70 per cent of starch. The gluten is readily separated from the starch in a proximate manner by kneading the flour under water in a thin cotton bag. In this manner the flour is filtered out and the gummy nitrogenous substance remains in the bag. Hard wheats are particularly valuable in the manufacture of products like macaroni (also in bread-making) as a result of the relatively high content and composition of the gluten.

148. Classes of proteins. — A system of classification of the proteins in keeping with that of other chemical substances (the molecular structure of which is better known) is now impracticable. Classification is based largely upon solubility under certain standard conditions. Three principal groups of proteins are recognized, namely, (1) simple, (2) conjugate, and (3) derived.

The simple vegetable proteids include albumins, some

of which occur in seeds and in cell-sap, such as leucosin of many cereals, legumelin of legumes, and ricin of the castor-bean. Such proteins are generally soluble in water. Globulins are soluble in salt solutions, but practically insoluble in pure water; such are legumin of many legumes, amandin of nuts, tuberin of the potato, and many others.

The conjugate proteins are so named because of the apparent association of two substances in the molecule (nucleic acid and protein in the case of nucleo-proteins) or of the ready separation of the molecule into these two substances. The nucleo-proteins are of much importance as constituents of nuclei.

Derived proteins, such as the proteoses and peptones, are considered more particularly under digestion, and may be regarded as the digested and diffusible products demanded by the cell for direct use in assimilation.

149. Amides. — Amides are also well known in plant tissues. Among these asparagin is of frequent occurrence. As a rule these compounds are not a storage form of nitrogen. They are commonly produced, and may accumulate to a considerable extent, during germination; from 10 to 30 per cent of the nitrogen in this form is not infrequent at that time. Leguminosæ may contain these compounds in exceptional amount, 75 per cent of the total nitrogen in vetch during germination being thus reported by Schultze. It may be regarded as a degradation product of protein, a product which is readily diffused, and again used.

150. Organic acids. — Organic acids are common constituents of plant juices. They may occur free or combined with mineral bases. As a result of the presence of

free acids and acid salts the cell-sap may be acid in reaction.

These substances may be looked upon usually as the by-products of metabolism, but they may be serviceable and some may function further in general metabolism. The group of fatty acids is well represented among the compounds in plant tissues; but the acids of commoner occurrence are the related oxalic, malic, tartaric, and citric, all being oxidation products of glycols (dihydroxy-derivatives of the paraffins).

Oxalic acid is of widespread occurrence, and it is most familiar (in the form of calcium oxalate) as the raphides or needle-shaped crystals so common in many vegetative organs. Malic acid is well known in many unripe pomaceous and stone fruits, but it occurs far more commonly, especially in "fatty" plants like the stone-crops; and it is the substance found by Pfeffer and others to be chiefly responsible for the "attraction" directing motile sperms to the egg-cells of certain ferns. Tartaric acid is readily extracted from the grape, in which fruit it occurs as acid potassium tartrate. Citric acid may constitute from 6 to 7 per cent of the juice of lemon, and it is also more abundant in the other species of Citrus than in higher plants generally.

The production of acids is usually favored by the abundance of soluble carbohydrates in the tissues. Submersed in a solution of glucose, for instance, the leaves of Oxalis rapidly increase in acidity. Among the lower plants, fungi and bacteria, the production of organic acid is even more common than with the higher plants, as again referred to under fermentation phenomena.

151. Tannins. — The tannins are bitter, astringent, water-soluble, amorphous substances widely distributed in the leaves, bark, and fruits of plants. All of these substances, which are of commercial importance, may be employed in the process of tanning skins and hides, since they form insoluble compounds with various nitrogenous bodies, giving a toughness and durability to the skin which constitutes the differences between leather and natural skin.

The tannins are alike in certain physical and chemical properties, but there may be dissimilarity in chemical composition. The tannin (glucoside) used in the making of leather is usually derived from the bark of various trees, including that of hemlock and oak, so extensively employed in the United States. The bark of hemlock may yield from 8 to 10 per cent of its dry weight of tannin and the leaves of tea may contain as much as 15 per cent.

Tannin is also extensively used as a mordant in the process of dyeing, for it produces colored products with various dye-stuffs; and it has long been employed in the manufacture of ink. The characteristic purplish brown color of the trunk of the cork oak from which the bark has been removed is due to this substance. The chief source of tannic acid (digallic acid) is a gall-nut produced upon an oak (*Quercus infectoria*), a product obtained for the most part from Turkey. Tannic acid constitutes more than one half of the dry weight of this gall. A similar product is yielded by a gall upon the sumac, *Rhus semi-alata*, which occurs in China.

Upon heating with sulfuric acid, tannic acid is hydrolyzed, yielding two molecules of gallic acid, thus, $C_{14}H_{10}O_9 + H_2O = 2\,C_7H_6O_5$. This process is also ac-

complished naturally by means of a few fungi, especially *Aspergillus niger*.

152. Resins and turpentine. — A great variety of products of physiological interest and of commercial importance are included in the groups commonly called resins and turpentine. They are produced in the cortex and young wood of a variety of plants generally characterized by special ducts or canals formed in connection with the conduction of these products.

The conifers furnish the chief commercial supply, and they constitute an important economic item in many of the coniferous forests of Europe and America. For a long time the balsams, especially the Canada balsam, have been a product of northern forests, whereas the turpentine industry has been best developed in the Southern States. According to Mayr a cubic meter of the splint wood of the standing tree contains approximately the amounts of fresh resins named, of which turpentine oil constitutes a considerable percentage, as follows: —

	Resins	Turpentine Oil
Pinus silvestris	21.1	60.0
Larix europæa	18.3	33.1
Picea excelsa	9.4	38.2
Abies alba	3.2	32.4

It is thus evident that the hemlock, which is poorest in solid resins, contains a very large per cent of the product as turpentine oil. The resins belong to the terpene series, but they occur along with various acids and other com-

pounds. Turpentine oil contains a large per cent of various volatile oils. The common method of turpentine orcharding has resulted in a great loss of timber due to the severe injury to the tree from the boxing and chipping employed. Methods have been suggested whereby this injury is now reduced to a minimum (Fig. 67). The crude products obtained by the method indicated are distilled, the volatile spirits being condensed, constituting turpentine, while the nonvolatile products are the solid rosins of commerce.

FIG. 67. Turpentine orcharding. [After Forest Service.]

153. Digestion. — The seed and the tuber are effective propagative devices,

because of the fact that they are at the same time storage structures. When, subsequently, conditions become favorable for the growth of the seedling or of the sprout, the seed or tuber is exhausted of its stored substances, which again move to the growing organs.

The starch and many other reserve foods stored in the tuber or in the endosperm of the seed are insoluble and indiffusible. It has already been indicated that for storage purposes solid or indiffusible forms may be necessary or economical. Nevertheless, such reserve foods, or the substances from which they were formed, enter the storage cells as diffusible products, and in such forms only can they find exit. The process of rendering organic materials soluble and diffusible, that they may be used in the cell or transferred to other cells and organs, or used in the building up of new substances, is digestion. It is a catabolic or breaking-down process, and the special nature of the changes involved is as diverse as the products acted upon.

From the preceding it is evident that when starch or any other insoluble food product is formed in the cells which are actively engaged in photosynthetic work, these products must undergo digestion before use or removal.

154. Digestion in different organisms. — Digestion in any cell or organ, in the animal or in the plant, is the same in principle. It is generally accomplished or accelerated by means of certain nitrogenous bodies or enzymes (included among catalytic agents) secreted by the protoplasm of the storage cells or the cells in the vicinity. In the vertebrate animal, digestion is effected through the secretion of digestive enzymes which enter the alimentary tract,

for the food-stuffs must be made soluble prior to direct absorption by the cells of the body. The parasitic fungus or bacterium may be able to dissolve and to penetrate the cell-wall. Then upon entering the cell the fungus may also gradually "appropriate" or digest the starch and other foods, absorbing them in this case, as does the higher animal, after digestion. It matters not what the organism may be which digests starch, the method is the same, and it is dependent upon the ability of the organism under the conditions to produce and often to secrete the starch-digesting or the starch-splitting enzymes. The same applies to other solid or indiffusible food substances, so that in general it may be said the use of all such substances as food is a factor of the specific digestive capacity of the organism, however simple or elaborate the digestive apparatus may be.

After all, the whole phenomenon of nutrition of even the green plant is not essentially different from that of the animal. The green plant makes its carbohydrate foods in certain cells, and it builds up nitrogenous substances out of these and inorganic nitrogen; but once sugar and nitrogenous bodies are formed, nutrition follows a course comparable in the two.

155. Enzymes and enzyme action. — The enzymes or soluble ferments are doubtless exceedingly numerous, and possibly the digestive enzymes alone are almost as many as the different kinds of reserve foods. So far as the study of these substances has progressed, they seem to be, for the most part, of protein character. At any rate, they are precipitated with proteins, yet certain analyses of the purified products disclose no nitrogen con-

tent, and much doubt is entertained respecting their precise nature. In general, however, they are regarded as protein. They show noteworthy differences among themselves, with regard to solubility, conditions of precipitation, and the like.

The enzymes are products of protoplasmic activity and are not generally regarded as readily diffusible; that is to say, the work of many of these is primarily within the cell where they may be produced. These are the intracellular enzymes. Nevertheless, in a number of cases there may be specialized secretory cells of some importance; and in other cases the digestion, or partial digestion, of products prior to absorption, is an indispensable character, as in the case of fungi and higher animals generally. Those enzymes which are active in part without, or beyond, the limits of cells producing them are termed extracellular enzymes.

The hydrolysis or decomposition of organic bodies like protein, starch, and fat under laboratory conditions (other than by the use of enzymes) is effected only by means of fairly strong acids, high temperatures, and other intensive agents. Contrariwise, the enzymes effect hydration and decomposition under the conditions of the plant cell or body, although their activity frequently reaches a maximum at 40° C. or slightly above.

A great majority of the commoner enzymes act by hydration; thus the effect of invertase upon cane-sugar is as follows: —

$$\underset{\text{Sucrose}}{C_{12}H_{22}O_{11}} + H_2O = \underset{\text{Dextrose}}{C_6H_{12}O_6} + \underset{\text{Levulose}}{C_6H_{12}O_6}.$$

On the other hand, certain classes of enzymes, not here

particularly considered, are believed to act by oxidation, and simple, molecular decomposition may also occur. The products may be diverse, as is common, or alike, as when maltose is transformed into two molecules of dextrose.

From relatively recent work it has also become certain that enzymes are important in synthetical processes as well as in the analytical ways referred to. In the former case they are said to possess a reversible action; that is, for example, — contrary to the instance above cited, where cane-sugar may be hydrated with the production of hexoses, — the hexose molecules may be built up by means of an enzyme into the anhydride or disaccharid form. Reversible actions appear to be very common, but little definite information is available at the present time.

Direct sunlight is promptly injurious to enzyme action. Fermentation is also commonly weakened at temperatures above 50° C. and "death" may result above 70° C. Most toxic agents are injurious to enzyme action at concentrations much above the normal death-point of the protoplasm, but at considerable dilution acids or alkalies may be stimulating. While a weak percentage of alcohol and a saturated solution of chloroform may not be injurious, strong alcohol may be fatal, so that in the precipitation of enzymes by 95 per cent alcohol there may be danger of losing the product.

156. Carbohydrate enzymes and their products. — Of the many carbohydrate enzymes it is possible here briefly to consider only a few. Chief in importance among these are diastases (amylases), acting upon starch, the hydrolysis and splitting of which yields a series of dextrins,

and finally maltose — which is subsequently converted by the enzyme glucase into glucose.

The diastases are widespread, and two forms are distinguished according to the type of corrosion of the starch grain. Diastase of translocation occurs especially in the chlorenchyma of leaves, and it corrodes the grain almost evenly. Diastase of secretion, corroding the grain irregularly (Fig. 68), is that which occurs in storage organs generally, but especially in seeds. Apparently a third form, takadiastase, is the product of *Aspergillus Oryzæ* in its action upon wheat or rice starch. Allied to diastase is inulase, converting inulin into fructose.

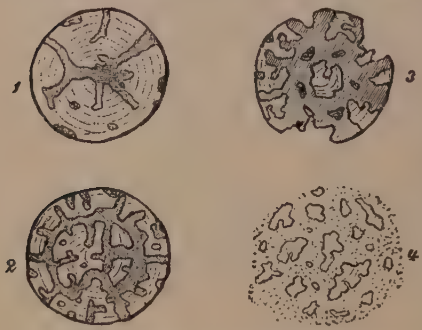

FIG. 68. Corrosion of starch grains by diastase of secretion. [After Strasburger.]

Cytase is a ferment often associated with diastase, as in the endosperm. It may be important in the dissolution of a certain "shell" of the starch grain. It is, however, best known from its action on the reserve cellulose, converting this into hexose sugars. It is probable that several enzymes are required in the decomposition of other celluloses, about which very little is known.

It has been indicated incidentally that the disaccharids sucrose and maltose are hydrolyzed and yield hexoses by invertase and glucase respectively. These enzymes are

widely distributed in both higher and lower plants. Both these and the diastases are most important in the production of malt used in brewing and distilling. The diastases are also important medicinally as an aid to amylose digestion, and many patented forms are on the market.

Another enzyme of special interest requiring further study is pectase, a form important in the hydrolysis of a portion of the cell-wall, producing a jelly from the pectic compounds.

157. Protein enzymes. — Protein enzymes were among the first to receive attention, and they have been more completely studied in the animal organism, where the action of pepsin in the stomach and that of trypsin received into the intestine from the pancreas are well understood. These enzymes must occur in plants, or else others which serve the same purpose.

Through ferments many proteins are converted into the more diffusible proteoses and peptones; while tryptic ferments may give a more complete digestion, reducing the peptone to the readily diffusible amido and amino acids, such as leucin and asparagin. Ferments which have been regarded as tryptic have been known for some time in plants, such as papain from the papaw, and bromelin from the pineapple. From recent work it appears that some of the so-called tryptic ferments may be, in fact, combinations of peptic and ereptic ferments. The last-named class is found by Vines to be well distributed in plants, and it decomposes the peptones with the production of amido and amino acids.

Doubtless many of the protein enzymes in plants are intracellular. The carnivorous plants, such as the sun-

dew and Nepenthes, secrete enzymes which act from without the absorbing organs, and likewise the fungi produce enzymes at least slowly diffusible. The exact method of action of the protein enzymes is not yet clear, but it is generally assumed to be hydrolytic. It is necessary that protein enzymes be produced in plants in some quantity at the time of germination to effect the movement and use of stored products, for, as has been shown already, indiffusible protein compounds are common in such organs. Moreover, at the maturity of the plant or of any vegetative organs of the plant much of the solid protein and protoplasmic material is converted and accumulated in the seed, and in the recovery of this from organs which have ceased to grow there is, of course, much economy.

158. Conduction of digested foods. — From what has been said regarding the action of digestive enzymes, it is apparent that there is required an effective means of translocation, as may be demanded, for digested materials to and from the leaves, shoots, storage organs, and seeds. Diffusible organic substances in complex plants seem to require, then, for rapid diffusion to and from active organs specialized paths or tissues. This demand is met through the phloëm of the vascular bundles, in which the sieve tubes occur (Fig. 6, *n*, *o*). The large protoplasmic connections between the rows of sieve cells evidently permit a movement more rapid than simple diffusion.

The sieve tubes are important in the movement of such products as shown by direct and indirect evidence: thus, by the fact that sieve tubes in particular contain a quantity of simple organic substances; by the absence of such products in so great a quantity in xylem, pith, or cortex;

by the interruption of conduction upon the removal of the phloëm; and by the failure of the loss of cortex to affect directly this movement of organic substances.

159. Ringing. — In horticultural practice ringing is applied to the removal of a small band of bark encircling the stem of dicotyledonous plants so as to include the cortex and phloëm. Sometimes there is made merely a circumferential cut through to the wood ring, or a small wire is bound tightly about a limb so as to cut into the bark, but these latter may heal too quickly to effect the result desired.

The principle is evident. Ringing interrupts the more rapid movement of digested foods toward the roots or basal parts to the detriment and often to the ultimate death of these structures; but there is an accumulation of foods above the ring, and this may be favorable for the developing fruit. This operation may result in a considerable increase in the size of the shoot, or in the production of tumors, above the incision.

Ringing is reported a widespread practice in Europe with grapes and apples, and it is employed to some extent in the United States. It should be used with caution where the plant is expected to serve future usefulness. It may, however, increase or incite productivity, hasten ripening, or enhance the size and quality of fruit. In the latitude of New York the grape is generally ringed during late June. The place of ringing should be between the chief fruiting canes and the main vine, but the exact location will be determined by the system of training. There should be such a development of canes below the ring as to fairly well nourish the main vine and root system.

LABORATORY WORK

Starch. — Examine under the microscope and describe the starch grains from a variety of sources, such as Canna (root-stock), potato (tuber), rice or oat kernel, milky juice of Euphorbia, and seed of beet. Leucoplasts associated with starch grains may be best observed in fixed and stained material, but they are also visible without staining in such favorable material as the young shoots of Canna, or in the young root-stocks of various monocotyledons.

Rub up about 1 gram of starch with a small quantity of water in an evaporating dish, and when there are no more lumps dilute to 50 cc. Is starch soluble in cold water? Heat the preceding to the boiling point, and when a paste is formed, examine it microscopically with respect to solubility.

With the paste above prepared, and with a weak alcoholic solution of iodine, make a complete test of the iodine reaction. In small test-tubes first use a few drops of a strong paste and considerable iodine solution, then weaken the paste up toward a dilution of one hundred times, using also less or weaker iodine. Determine the effect of heating and recooling, also of a few drops of strong caustic potash, upon the iodine reaction. Compare the reactions of the starch paste toward iodine with that of a suspension of starch in cold water.

Study the distribution of starch in any plant available, employing sections, especially from fleshy roots, leaves, etc. Determine where in the resting twigs of apple, lilac, or maple the storage of starch occurs. In order to stain starch occurring in small quantities in the tissues, especially in the cells of leaves, as of Elodea grown in weak light, or to bring out the starch in chlorophyll bodies, the material may be stained in a concentrated solution of iodine in potassium iodide, when the grains stand out black. Again, a dilute solution of iodine in potassium iodide may be used, and after washing, the material may be laid in a strong solution of chloral hydrate which dissolves most of the cell-contents, swells the stained grains, and in time decomposes these last also, so that a prompt examination must be given.

Inulin. — Make and examine sections (mounted in alcohol) from small pieces of the tuberous roots of Dahlia which have lain for a week or 10 days in strong alcohol. Describe the spherites observed. Treat the sections with cold water and examine, then treat with hot water, and discuss solubility.

Glucose and other sugars. — The most decisive test for glucose, other reducing sugars, and certain glucosides is the precipitation of cuprous oxide in Fehling's solution. The identification of the different sugars or other substances may require other tests.

Prepare Fehling's solution using two bottles as follows: *A*, 34.6 grams of pure crystals of copper sulfate dissolved in distilled water and made up to 500 cc.; *B*, 173 grams of Rochelle salt (potassium sodium tartrate) and 60 grams of sodium hydrate dissolved in distilled water to make 500 cc. In employing this test use always equal quantities of the two solutions.

Add to some Fehling's solution in a test-tube a small granule of glucose or a few drops of a strong solution. Boil the solution for three minutes, and describe the reaction. In the same manner test the juice of ripe grapes, or ripe plums or peaches. In this case note the rapidity of the reaction, to contrast with a later test of beet juice.

Use the Fehling's solution with a few crystals of cane-sugar. Is there any reduction? Boil the cane-sugar previously with a few drops of hydrochloric acid, neutralize with KOH (to litmus), and then repeat the Fehling's test. Discuss. Press out some juice of the sugar-beet, or grate up a small amount, and extract with water; then test this juice (or extract) with Fehling's solution, being careful to heat gently, since violent heating will, through other substances present, be alone sufficient to convert cane-sugar. Compare the result with that obtained when grape or peach is employed. Compare the reaction of crystals of cane-sugar and granules of glucose in a few drops of concentrated sulfuric acid.

Celluloses. — Crack a seed of date, make a section or shaving of the endosperm, and study the preparation with respect to the reserve cellulose deposited upon the cell-walls, describing accurately the nature of the cells in which such deposits occur.

Test the solubility of cellulose (cotton fibers) in concentrated sulfuric acid and in cuprammonia. In the first case use small quantities of the materials, rub up in a Syracuse watch glass, when dissolved neutralize with KOH and test for reducing sugar (glucose).

With half-concentrated sulfuric acid determine the length of treatment required to yield a blue color with iodine.

Place cotton fibers, sections of a root-tip, etc., in a solution of chloriodide of zinc (dissolve chloriodide of zinc in less than its weight of water and add metallic iodine until a bright cherry color is produced). Place the material in the concentrated solution, examine under the microscope, and describe the characteristic color reaction.

Fats and oils. — The fats and oils are generally soluble in ether, chloroform, benzene, and other solvents of this nature, and certain oils (castor oil) in absolute alcohol. Examine sections of the endosperm of castor-bean and of the garden bean in water; then after immersion for a few minutes in absolute alcohol and ether, reëxamine. Stain similar sections from a few minutes to half an hour with a 50 per cent alcoholic solution of cyanin (or in a solution of alcanna in absolute alcohol, then diluted to 50 per cent) and note the deep color of the oily bodies.

Proteins. — Proteins may be soluble in water, in salt solutions, in alcohol, and in acids and alkalies. Make sections, or shave off with the razor fragments from the endosperm of wheat, mount in water and examine for "aleurone" grains (not soluble in water) in the outer layer particularly. In the same way examine sections of the endosperm of castor-bean for protein crystalloids and globoids, preferably after removing the oil (in this case) by immersion for a few minutes in absolute alcohol.

Mix some wheat flour and water, place in a cloth bag and knead under a stream of water at the faucet. The glutinous dough resulting after the starch is washed out is the gluten of wheat, consisting of a mixture of protein substances some of which, in the living cells, are indistinguishable from the cytoplasm. Take a small portion of this gluten, rub it up with a 2 per cent salt solution, and save for later study. Test the sol-

ubility of another portion of the gluten in 70 per cent alcohol and save the solution. Use a part of this solution for an observation upon coagulation by diluting the part taken to three times the volume with distilled water.

Grind up three grams of beans extracted with 30 cc. of water in a test-tube, shake occasionally for 10 minutes, filter, and employ the filtrate along with the preceding solutions in some of the tests given below. A portion of this filtrate, however, may be tested as to coagulation in two ways: (*a*) acidulate a small amount in the test-tube and apply heat; (*b*) add to a few cubic centimeters in a test-tube four times the volume of 95 per cent alcohol.

The following are some reactions of proteins which are in part distinctive: —

1. Brick or rose-red color with Millon's reagent on standing, or with gentle heat. [To prepare Millon's reagent dissolve 1 gram of mercury in 2 grams of nitric acid (1.42 s. g.), and then dilute with twice the volume of water.]

2. The Biuret reaction, a violet or purple color with copper sulfate and sodium hydrate. To a very weak copper sulfate solution add excess of potassium hydrate and apply heat, then add a small amount of a protein solution and heat again.

3. Yellow color on boiling with nitric acid, the xanthoproteic reaction. After boiling, cool under the faucet and add ammonia, when the color will change to orange.

4. Violet color with acetic and sulfuric acid. Use 2 parts glacial acetic and 1 part sulfuric acid, with a small amount of protein material, and apply gentle heat.

Starch digestion. — Several forms of diastase may be obtained as commercial products, but it is well to undertake the extraction of one or more of these in the laboratory. Take 200 grams of clean barley seed, soak in running water over night, and germinate in a thick layer over moss until the roots are about 1 inch long and the plumules well started. Dry at 40 or 50° C. for about six hours. From this malt the diastase of secretion is to be obtained. In the same way collect (preferably an hour or two at least after sunset) about 200 grams of nasturtium, bean, or

potato leaves and dry in the same manner. These will yield diastase of translocation (ungerminated seeds of barley likewise). Grind the products separately (also powder the leaves) and extract for 24 hours with two times the weight of 20 per cent alcohol. Filter the alcoholic extract and precipitate the crude diastase (along with some other proteins) by adding 2½ parts or more of 95 per cent alcohol. After a short time filter to collect the precipitate. Dissolve the first (from barley seed) in 50 cc. of water, and the second (from leaves) in 25 cc., adding to the first 2 cc. chloroform, and to the latter 1 cc., to inhibit the growth of bacteria.

Make about 200 cc. of 1 per cent starch paste (from rice starch), and into each of three test-tubes pour 25 cc. of the starch paste, labeling the tubes, *A*, *B*, and *C*.

To tube *A* add 5 cc. secretion diastase.

To tube *B* add 5 cc. translocation diastase.

To tube *C* add 5 cc. distilled water.

At intervals of ¼ hour shake the tube, take 1 cc. samples, and test with iodine, noting the changes of color (as dextrins are produced) from blue through purple to wine-red, finally colorless. When the starch reaction has disappeared, note the change in appearance of the solution. Test with Fehling's solution for reducing sugar.

Drop a small quantity of potato starch into a few cubic centimeters of each of the two diastase solutions (translocation and secretion) in two vials, slightly acidulate with weak HCl, and after intervals of an hour or so study the types of corrosion.

If time permits, compare the effects of high and low temperature, bright and reduced light, and strong and weak acids upon diastatic action.

Translocation. — Verify the previous indications respecting the use of starch by the leaf or loss from the leaf when placed in the dark. Employing a Fuchsia (as previously used, page 223), geranium, or nasturtium, secure a plant which has been exposed to bright light three hours or more, so that abundant starch occurs in the leaves. Select two or three healthy leaves and on one side of the midrib, or middle, of each sever completely the main

nerves or veins. Place the plant in the dark for four hours, or over night, then dissolve out the chlorophyll, apply the starch test, and discuss the results with respect to translocation.

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CHAPTER XII

RESPIRATION, AËRATION, AND FERMENTATION

The importance of air in the maintenance of animal efficiency has been recognized as long as mankind has existed. Shortly after the discovery of oxygen by Lavoisier and Priestly (1774), Scheele showed that air exhaled by animals contains a smaller proportion of oxygen and an increased content of carbon dioxid. That marks the beginning of our knowledge of one of the products of respiration and of the extensive use of oxygen (O_2) by active living things. It was not, however, until later that the relation of plants to oxygen was understood; and at that time, of course, the fundamental nature of the catabolic or destructive changes taking place with or without free oxygen in both animal and plant cells could not be suspected.

160. The term "respiration." — Long before there was any accurate knowledge respecting the nature of the chemical changes (whether anabolic or catabolic) which may proceed in the cell, the term "respiration" was in use to denote in animals "breathing," — this latter term never aptly applying to any part of the process in plants. With the progress of physiological study upon plants and

animals the "heat of respiration" and the "energy of respiration" became well-known terms, so that respiration acquired a significance far wider than at first. In spite of this, the mechanism effecting gas exchange and the production of certain of the more common products of respiration (CO_2 and water) long received consideration as respiration. In more recent times the determination that the fundamental changes involved are those taking place in the living cells themselves has therefore stretched further the use of this term. In both animals and plants these changes — alike in kind — are the essential features of respiration.

At present there is a clear distinction between the usual oxygenating or aërating processes[1] and the energy-releasing changes occurring in the cell. These last have been termed "energesis," — a term differing from catabolism chiefly in its more limited application and in laying emphasis upon the current view of the chief effect of respiration.

161. An obvious result of respiration. — If an animal is given no food-materials, even for a single day, it must lose weight, although it may be supplied with the normal amount of water. A green plant placed in distilled water, and deprived of light — the essential condition for the making of organic food — will lose from day to day in dry-weight of its substance. Similarly, seeds germinated in darkness may, with requisite water, increase many times in bulk; but the dry-weight will constantly decrease, — so rapidly, in fact, that quickly germinating seeds may lose

[1] The suggestion that these alone should be called respiration seems inadvisable.

in two weeks half their original substance, the expelled products being mostly CO_2 and H_2O.

This loss of organic substance is indicative of respiration, a process of catabolism and energy-release absolutely essential for the maintenance of every active cell,— plant or animal, — in both of which the essential process is substantially the same.

162. The demonstration of respiration. — It is not at all requisite that respiration shall have exactly the same course in the cells of different organisms, nor is it necessary that it shall be dependent upon a common type of mechanism for the usually accompanying gas exchange.

Once properly understood, activity and growth are themselves the best evidences of respiratory activity. Nevertheless, there is a gas exchange commonly inseparable from the process, and this gas exchange, since it is an accompaniment of respiration, serves as a simple and definite demonstration of the material end result, or of the type of material change which goes on. This gas exchange consists in the absorption and use of O_2 and the elimination of CO_2. Most important as a provisional experimental demonstration of respiration is the evolution of CO_2. This is, of course, positive indication that organic matter is undergoing catabolic or dissimilatory transformations, and the CO_2 set free may be made, usually, a satisfactory qualitative or even quantitative measure of the comparative rate of the process, especially in the higher plants, with which we are particularly concerned.

Proof of O_2 absorption and CO_2 production during the activity of living tissues is most definitely shown by an accurate analysis of the gases from a respiration chamber.

This may not be practicable for the present purpose, and a simple suggestion of these gas relations is brought out by means of the often misused experiment with germinating seed. In this experiment the seed are placed in two bottles or jars carefully corked or sealed. After the lapse of a few hours a lighted taper lowered into one jar will be extinguished, and at the same time a thick film of barium carbonate will form on baryta water in a dish introduced into the other jar. (This film is far more pronounced than that which would form upon a similar test in a control jar containing air.)

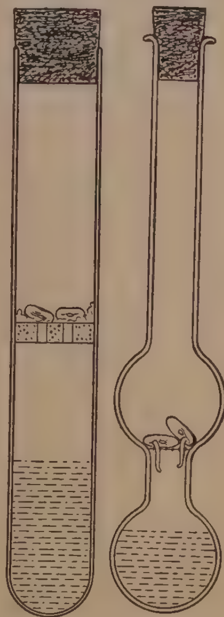

FIG. 69. Simple respiroscopes.

The above experiment suggests definitely two things: (1) that the content of CO_2 has been increased, and (2) that oxygen has disappeared; but neither this nor any other simple experiment, unfortunately, affords convincing proof that no other change takes place.

A far better demonstration of the evolution of carbon dioxid is obtained by employing growing seeds in other types of apparatus, two of which may be briefly referred to: (1) by germinating seeds in a bottle or test-tube over baryta water (Fig. 69), or in a chamber in which a dish of baryta water is placed, and by comparing the amount of the precipitate in this respiration chamber with that in

a control vessel lacking seed; (2) by drawing air deprived of CO_2 through the respiration chamber, and catching the CO_2 given off in a wash-bottle of baryta water. For quantitative work it is absolutely necessary to study standard methods of CO_2 determination and to employ these with all the chemical precautions required; especially important is a gravimetric method in which the CO_2 is caught in potash bulbs.

The rapid inhibition of growth in the absence of oxygen may be taken as indicative of the use of this atmospheric constituent. The effect upon growth of an atmosphere deprived of oxygen may be demonstrated by a comparatively simple experiment in which germinating seeds are placed in a tube containing normal air, and this is compared with another from which the O_2 (and CO_2) are absorbed, as explained in the laboratory instructions.

163. Respiratory phenomena in aërobic respiration. — In the type of respiration thus far particularly considered oxygen has free access to the respiring cells, and it is used in promoting chemical changes. This is called aërobic respiration, as distinguished from anaërobic respiration (subsequently discussed), which proceeds in the absence of free oxygen.

The following may be given as a concise summary of the aërobic respiratory phenomena including the accompanying gas exchange in green plants: —

(1) Along with other gases, oxygen diffuses into the tissues, it is absorbed by the cell-sap, and it reaches all parts of the protoplasm of the cell.

(2) Oxygen promotes catabolic processes, and whether through the protoplasm and its constituents directly, or

chiefly through foods associated with the protoplasm, it takes an active part in the chemical changes of the cell, as a result of which the ultimate excrete products CO_2 and H_2O may be formed.

(3) Complex organic molecules are decomposed; thus simpler products are produced, and kinetic energy is released. A part of this energy is in some manner utilized by the plant in growth and other activities, while another part, set free as heat, has little or no obvious value.

(4) Of the final excrete products of this series of changes, the most significant is carbon dioxid, and it is eliminated from the tissues by the general diffusion mechanism involved in the entrance of gases.

164. Oxygen promotes catabolic processes. — The studies which have been made upon the decomposition and hydrolysis of protein and other foods and the identification of oxidizing and hydrolyzing enzymes as of widespread occurrence in cells point clearly to decomposition as the essential nature of the process. By some the decomposition of the protoplasm (cf. Barnes and others) is regarded as most important, while others view the process as essentially, or at least in part, a decomposition of foods, including carbohydrates and fats. Neither view is at present entirely satisfactory, but it is not possible here to review the evidence. It is certain, however, that the presence of free oxygen involves ultimately the decomposition of less material and a more economic energy-release. Moreover, normal respiration, and consequently the growth of most plants, is promptly checked by even the temporary exclusion of free oxygen.

165. The ratio of O_2 absorption to CO_2 production. — By

many physiologists respiration has long been considered to be a combustion process. If by combustion one understands a direct union of the O_2 with C in such a manner that CO_2 is a direct result, this comparison is unfortunate. The combustion of any product results in a perfectly definite amount of energy as heat; and this heat-energy may be very simply determined, whether it involves the combustion of coal, of proteins, of starch, or of cane-sugar. There is, furthermore, in combustion (however produced) a definite relation between the amount of oxygen needed and the amount of carbon dioxid given off. There is therefore a definite CO_2 / O_2 ratio; thus the combustion of glucose would require 6 molecules of O_2, and 6 molecules of CO_2 would be produced, by the following formula: —

$$C_6H_{12}O_6 + 6\ O_2 = 6\ CO_2 + 6\ H_2O.$$

The combustion quotient in this case is unity. In respiration the transformations are not necessarily complete, and the respiratory quotient is seldom exactly unity, and as a consequence there are by-products and products less stable then CO_2. The quotient is affected by temperature and other environmental conditions; thus it is possible to picture a more complex and less definite sequence of changes in which protoplasm is involved. The series of transformations may be of the same type in the two cases, but they are not properly regarded as comparable processes so far as may be determined at present.

166. **Respiratory activity.** — Respiratory activity is greatest during periods of rapid growth and differentiation. So soon as adequate water is absorbed by seeds previously

dried, active respiration begins. The curve of CO_2 excretion depends upon various external conditions, but a maximum is generally obtained by the time shoot and root are fairly elongated, after which there may be a rapid or gradual decline until the seedling is well developed. The curve shown (Fig. 70) is made up from data given by Mayer, and it shows the results with seedlings of wheat at a temperature of 23.8° C.

This curve may be taken as merely a sample of the respiratory rate during germination, although the curves for other seed may not be closely conformable. Frequently the rate of respiration for germinating seeds is, with respect to weight, about equivalent to that of man, generally given as about 1 per cent of the body weight for 24 hours. Seeds which germinate rapidly may, however, lose, under favorable conditions, one third of their dry-weight during a period of 10 days, which is an average of about 3 per cent per day. In such cases, therefore, the intensity of respiration is relatively greater than for many warm-blooded animals.

As the embryonic tissues in the plant are relatively reduced, the respiratory ratio will fall, so that well-developed plants, or those growing slowly, will show, with respect to body weight, an exceedingly low ratio. Plants or organs passing into a resting stage will fall to a minimum which, in the case of dry seeds and well-protected bulbs, may approximate zero. On the other hand, opening flower-buds may show a high respiratory activity, often relatively greater than at the time of germination. According to Pfeffer, rapidly growing bacteria may consume oxygen at a rate 200 times as rapid as required by

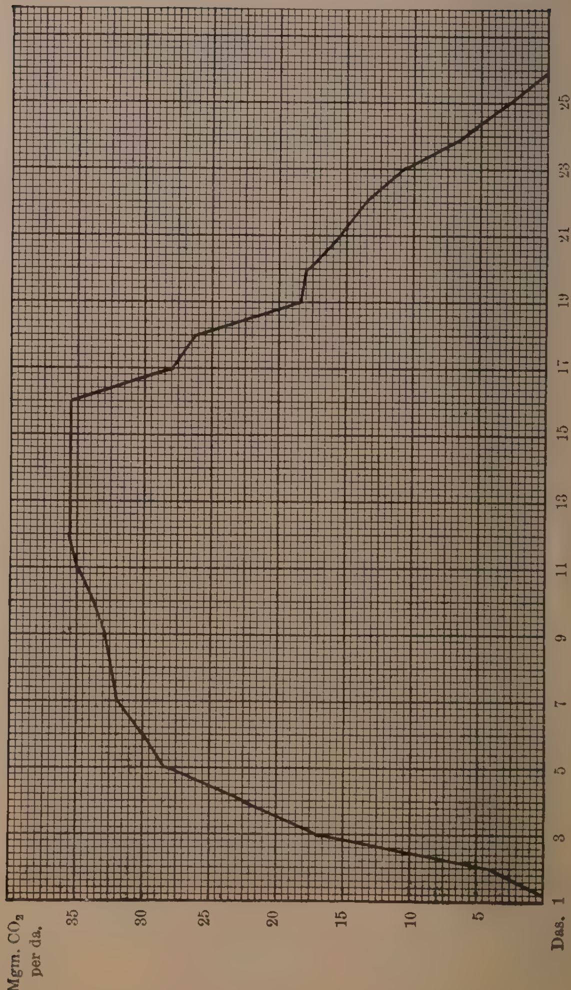

FIG. 70. Germination of wheat; curve of CO_2 excretion at 21° C. [After Rischawi.]

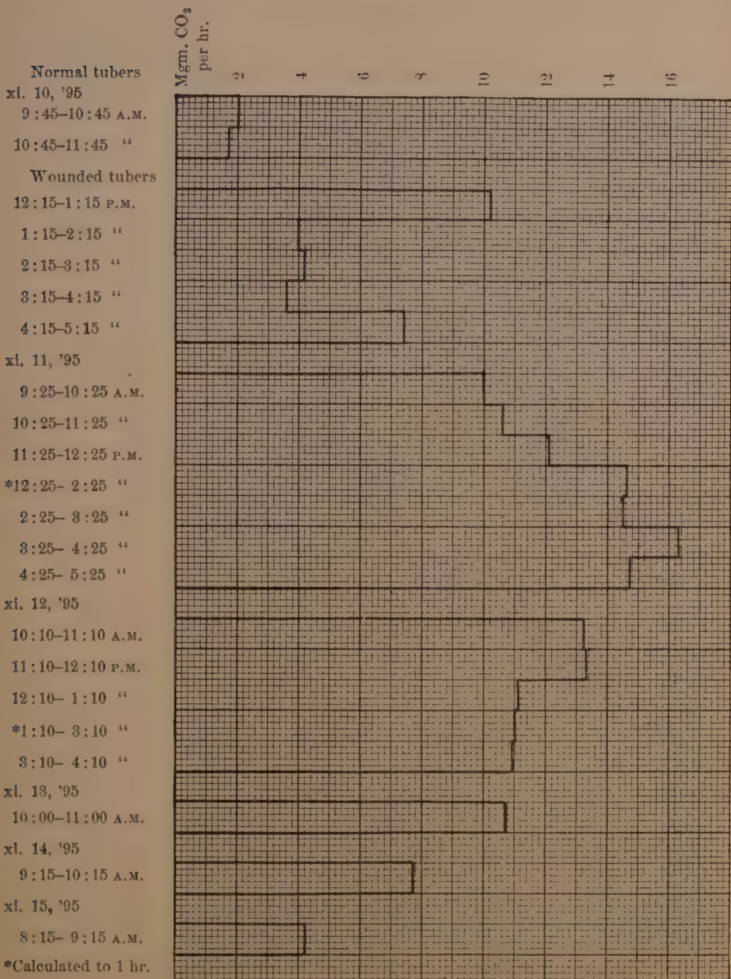

FIG. 71. Chart of CO_2 excretion, normal and wounded potato tubers. [Data from Richards.]

man, and this fact is significant with respect to the importance of these organisms in the general disintegration of organic materials.

167. Respiration of wounded plants. — It has been repeatedly demonstrated that the respiratory activity is increased by injuries to the tissues. Precise data upon this point have been contributed by Richards. He employed chiefly potato tubers, but the experiments with these tissues were supplemented by carrot roots, also certain seedlings, leaves, and willow-twigs. In general, it is found that following injury there is increased respiration for a time. Usually after two days — under the conditions of the experiments — the activity again declines to a rate more nearly the normal. The chart (Fig. 71) shows the CO_2 developed from the respiration of 24 small potato tubers (weighing 200 grams) before and after wounding, the wounding consisting of slicing the potatoes lengthwise.

The ordinates represent milligrams of CO_2, and the abscissæ, time intervals of one hour each, on parts of several succeeding days as indicated. The sudden rise in CO_2 production after the injury of such solid tissues is explained by the inclusion of CO_2, which is then rapidly lost during the first two or three hours.

168. Heat release. — Exact determinations of the heat release in plant respiration have not been possible with the experiments as generally conducted. It has long been shown, however, that the temperature inside of the respiration chamber containing germinating seeds, opening flower-buds, and other materials exhibiting vigorous respiration may be 5 or 10° C. above that of the surrounding

air. In rough experiments, however, much of the heat is lost by radiation, and such data are merely suggestive. Complex calorimeters are in use to measure the heat of animal respiration, and recently an advance has been made in simple plant experimentation by the use of the doubled-walled silvered Dewar bulbs, or thermal bottles. In preliminary experiments without sterilization precautions, Peirce secured a rise of temperature with an unweighed quantity of peas (in a silvered 250 cc. Dewar flask) amounting to about 25° C. in three days, with a maximum rise of about 40° C. reached on the seventh day. With sterilization precautions and employing in 250 cc. silvered Dewar flasks, 300 seeds of Canada field peas, a maximum difference of about 20° C. has been observed in some class tests. This does not represent the actual differ-

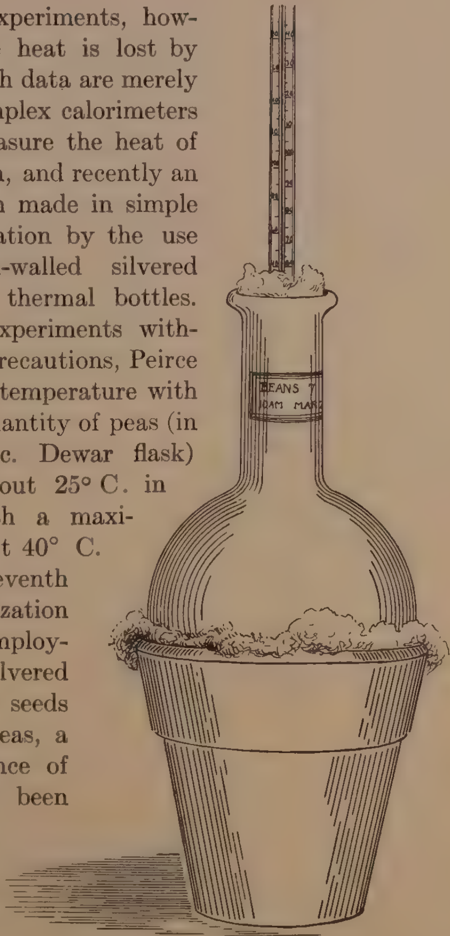

Fig. 72. Dewar bulb.

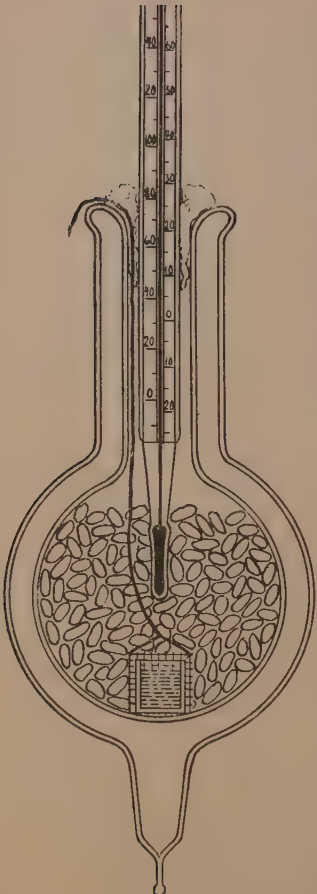

Fig. 73. Dewar bulb in cross-section, showing also method of experiment, — heat release.

ence, since heat is lost even from the silvered flasks. It is greatly to be desired that an accurate calorimeter may be perfected.

169. The mechanism for gas exchange. — To a considerable extent, the histological mechanism permitting the diffusion of oxygen through the tissues of the plant is the same as for carbon dioxid used in photosynthesis. Nevertheless, the cells active in photosynthesis are localized, in higher plants, and the mechanism which permits aëration, in general, is more complex and may be treated.

Since respiration is proceeding in every living cell, the possibility of a fairly rapid gas diffusion must extend to the remotest tissues. In developing or mature roots, stems, leaves, and fruits, there may be found considerable intercellular space providing for diffusion

of gases; sometimes indefinite air chambers form in a variety of ways. The intercellular spaces are produced by the splitting apart of the walls separating meristematic cells, generally at the angles. In this way, small spaces are produced into which air diffuses, and when such spaces are numerous, they form practically continuous air chambers. In some cases these spaces occupy far more volume than the cells themselves. This is particularly true in the case of the mesophyll tissue of leaves.

FIG. 74. Experiment suggesting the efficient aëration of the leaf. [After Detmer.]

Very large air spaces are a characteristic feature of many water plants, and they are often accompanied by a peculiar distribution of the cells, or of irregular or stellate out-growths from these into the cavities at a later period. Again, during the process of growth, cavities may arise

through the more rapid growth of certain regions, and the rupture of cells adjacent, as in the case of certain grasses, and of many other plants generally possessing a loose central pith during the early stages of growth. In the more solid or woody stems, intercellular spaces constitute some part of the structure, and the better aërated cortex may be provided with lenticels, or special areas of loose tissue permitting gas exchange. These lenticels are interruptions of the more or less continuous corky envelope constituting an essential part of the true bark of many woody plants.

Roots may, in general, obtain some oxygen in solution, but the cortical parts of these organs exhibit, as a rule, rather large intercellular spaces, so it is evident that this special type of diffusion mechanism for aëration is important likewise in subterranean organs. In fact, in many roots there may be found special tissues, apparently insuring a surplus of air, and such may be designated air-storage tissues. Certain plants inhabiting stagnant water are provided with special roots, or root branches, which seem to be important in aëration. To these organs the term "hydathodes" has been applied.

The relation of leaf-stalk and blade to air or the continuity of the aërating tissues may be very well emphasized by the experiment shown in Figure 74, in which, when suction is applied to the tube, air passes through the leaf, and is given off in bubbles from the petioles below the surfaces of the water in the bottle.

170. Anaërobic respiration. — It has been clearly demonstrated that respiration may proceed for a time, in most tissues and cells, when no free oxygen is available.

Considerable diversity may be manifest as to the extent of this respiration, and in the case of germinating seeds, the nature of reserve foods is an important factor in this regard. In certain tissues, anaërobic respiration takes place to such an extent as to be very readily recognized by the usual demonstration of CO_2 production. Nevertheless, while CO_2 is commonly an end product of this type of respiration, alcohol, lactic acid, hydrogen, and other products may be identified with it. Since no free oxygen is required, decomposition resulting in CO_2 and the other products mentioned are obviously by rearrangement of the atomic groups in the organic molecules. This type of respiration is therefore truly anaërobic, or without aëration. The term "intramolecular" has also been employed in this connection.

Anaërobic respiration in the tissues of higher plants may be experimentally studied by use of germinating seeds, preferably starchy seeds, such as barley and buckwheat, but slices of potato or other solid tissues of this nature are also useful. The essential apparatus is the same as for aërobic respiration, but in this case it is necessary either to exhaust all air with a first-class air pump, or else to replace air with some gas which is physiologically inert. Hydrogen was formerly used as a gas of this nature, but as there is a possibility that it may be so injurious as to introduce error, nitrogen may be substituted therefor.

Attention has been drawn already to the fact (section 87) that anaërobic respiration of roots is found to result in the production of traces of some excrete organic acids, whereas, in aërobic respiration, CO_2 alone is evolved. All of the results point to the conclusion, therefore, that by-

products and wastes are far more abundant in anaërobic respiration, owing to the lack of oxygen to stimulate the changes resulting in the production of CO_2 and water. With respect to micro-organisms which frequently demonstrate anaërobic respiration, this subject is further discussed in succeeding sections upon fermentation.

171. Fermentation. — The original significance of this term had reference to decomposition or change in organic substances, such as sugar solutions and cider, accompanied by the evolution of bubbles of gas, and generally by the production of alcohol. After the work of Pasteur and others, it was apparent that such changes (although they may be due ultimately to enzyme action) are in consequence of the activity of micro-organisms, which are then defined as having the capacity to ferment certain substances.

In more recent times the term has applied to a variety of types of decomposition due to microscopic organisms, and also to the action of a large class of enzymes (soluble ferments), whether obtained from micro-organisms or from higher plants. The "ferment" action of the great majority of enzymes does not involve the liberation of CO_2.

In general, fermentation phenomena may be regarded as representing the various steps in decay. The type of fermentation in any particular case is usually given the name of the chief product produced, although in some cases it is the group of substances acted upon which stands sponsor for the name. In this chapter, only a few of those fermentation phenomena are discussed that are induced by the growth of micro-organisms, and as a result of which alcohol and certain acids are produced.

172. Lactic fermentation. — If no precautions are taken to prevent the contamination of milk as it is drawn from the udder, it normally undergoes lactic fermentation, at the temperature of the dairy or living room. Among the organisms usually finding access to the milk, are bacteria (especially *Bacterium lactis acidi*) the action of which produces a slight acidity or souring, and later a marked effect exhibiting itself in the precipitation of the casein (curdling). The acid developed is largely lactic, and the course of the main changes referred to, involving the milk sugar (lactose, which is first converted into hexose sugars), is probably substantially thus: —

$$\underset{\text{lactose}}{C_{12}H_{22}O_{11}} + H_2O = \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{galactose}}{C_6H_{12}O_6} = \underset{\text{lactic acid}}{4(C_3H_6O_3)}$$

One or more of a variety of organisms produce this end result. In general, they utilize as food a portion of the sugar, and they may produce, in small quantities, beside lactic acid and carbon dioxid, the following: one or more of several organic acids, also hydrogen, nitrogen, and traces of methane, depending somewhat upon environmental conditions. The production of lactic acid is so rapid in milk that the medium is soon sterilized with respect to the presence of other organisms; but this is scarcely an advantage to the lactic forms, since this fermentation and the activity of the lactic organism is usually brought to a standstill when about .8 per cent of acid has been produced. According to certain investigators, a small amount of lactic acid as an excrete product may be produced during the anaërobic respiration of roots.

173. Alcoholic fermentation. — Alcoholic fermentation

is more commonly brought about by the growth of various species of yeast in liquids or moist substrata containing certain sugars. Some organisms show a marked specific election with respect to the sugar fermented; but in general, the hexose forms are most important, while trioses and nonoses are sometimes used. When abundant O_2 is supplied, the yeasts may grow rapidly, utilizing the sugars as foods, and effecting relatively little fermentation. In the absence of sufficient O_2 for rapid growth the organisms grow slowly, but fermentation proceeds vigorously. The decomposition of glucose yields ethyl alcohol and carbon dioxid as chief products, expressed conveniently by the following equation: —

$$\underset{\text{glucose}}{C_6H_{12}O_6} = \underset{\text{ethyl alcohol}}{2(C_2H_6O)} + CO_2$$

On account of this capacity to produce alcohol, yeasts are the important organisms utilized in the production of alcoholic beverages, and the proper regulation of growth and fermentation is the essential factor in economic production. Starch, cane-sugar, and other carbohydrates transformable into the fermentable types are, of course, ultimately used, if first hydrolyzed, as in the malting process.

Yeasts are unusually resistant to the alcohol produced, but the fermentative activity declines rapidly at 12 per cent, and at 14 per cent there is usually complete inhibition. This concentration, however, is far greater than that which the more resistant molds may endure, commonly from 4 to 5 per cent. It is well known that the production of CO_2 bubbling through and held by the cohesive

gluten of wheat flour, is the important factor in light-bread making. It is of interest to note that anaërobic respiration in higher plants results in the production of a small amount of alcohol, so that the two processes are comparable.

174. Acetic fermentation. — Acetic fermentation in nature generally follows the alcoholic, and it is brought about by the so-called acetic bacteria. These organisms effect the oxidation of ethyl alcohol in weak solution to acetic acid, probably in two steps, with the following, general result: —

$$\underset{\text{ethyl alcohol}}{C_2H_5OH} + O_2 = \underset{\text{acetic acid}}{CH_3COOH} + H_2O$$

At the same time some alcohol is utilized and CO_2 produced. In commercial vinegar-making, cider, weak wine, and other products of this nature are utilized, and there is a slow and a quick method of procedure depending upon the aëration.[1]

LABORATORY WORK

Loss of weight. — Select two lots, each of 25 seed, of peas or beans. Determine the dry-weight of one lot and record. Soak and germinate the other lot in the dark closet upon a plate containing moist filter paper. When the seedlings have grown about as long as they will from the food material of the seed, determine the dry-weight and compare with those ungerminated.

Absorption of O_2 and evolution of CO_2. — Into jars or wide mouth bottles put some soaked or germinating seeds of peas or beans, and cork tightly or seal. After a few hours, or next day,

[1] Prescott, S. C., "Wine, Cider, and Vinegar," Bailey's Cyclopedia of American Agriculture, **2**: 181–186.

test the air in one with a lighted wax taper and in another with a small dish of baryta water, comparing with similar tests carried out in a bottle containing only air. Explain the results and indicate the limitations of the experiment.

Evolution of CO_2. — Pour some baryta water into a large test-tube, then introduce a closely fitting perforated cork upon which two or three germinating seeds may be placed; cork and seal (Fig. 69). Set up a control experiment without the seeds; in a few hours compare and discuss the results with respect to the baryta water.

Set up an apparatus as suggested in section 162 consisting of a chamber with germinating seed, or other favorable material, connected on the side toward the inflow of air with two wash bottles of potassium hydrate, to take out the CO_2 of the air, and on the side toward an aspirator or filter pump with two bottles of baryta water,[1] for the demonstration of any CO_2 given off. Before connecting up with the baryta water bottle draw air through the apparatus to remove the normal air. Connect with the baryta bottle, darken the respiratory chamber [Why?], and draw air through the entire series for an hour or two. Describe the result.

In quantitative work a standard method of CO_2 determination should be employed, preferably a gravimetric method, in which potash bulbs are used, protected as to acquisition and loss of water by calcium chlorid drying tubes. In order to demonstrate anaërobic respiration in seed or other material the most satisfactory simple method is to replace the air in the apparatus with hydrogen. For this purpose a hydrogen generator is required in connection with the other apparatus described. There is evidence, however, that nitrogen is preferable to hydrogen, but in most laboratories it is not practicable to employ this gas.

Heat release during respiration. — Soak for about 12 hours

[1] Make a concentrated solution of barium hydrate, with excess of the barium salt, keep the bottle or flask well stoppered, and decant off or pipette out the liquid, when needed, avoiding all unnecessary exposure to the air.

somewhat more than 200 grams of field peas or wheat, and after soaking weigh out two lots of 100 grams each. Kill one lot by immersing it in boiling water for about 10 minutes, then place both the killed and the living seed in separate cheesecloth bags and immerse each in formalin solution (1 part to 600 parts of water) for 15 minutes. Take the bags from the formalin and dip them into boiled water with as little handling as possible (the water should be at room temperature or at the temperature of the incubator to be used). Have thoroughly cleaned by the chromic acid mixture two double-walled, vacuum, silvered flasks or Dewar bulbs of 250 cc. capacity (Figs. 72 and 73). Sterilize these also by rinsing with the formalin solution above indicated. Provide each flask with a short vial or small dish of KOH protected from tipping over by a wire cage lowered by a string, also previously sterilized as to the exterior. Pour carefully each lot of seed into a separate Dewar bulb, insert a standard thermometer, previously dipped in formalin and rinsed, and plug the flasks with wool. Wrap the flasks well with felt or woolen cloths and place them at a temperature as constant as possible. Ten minutes later take the temperature of each, and at intervals of 12 hours for several days, or until there is a rise of temperature in the

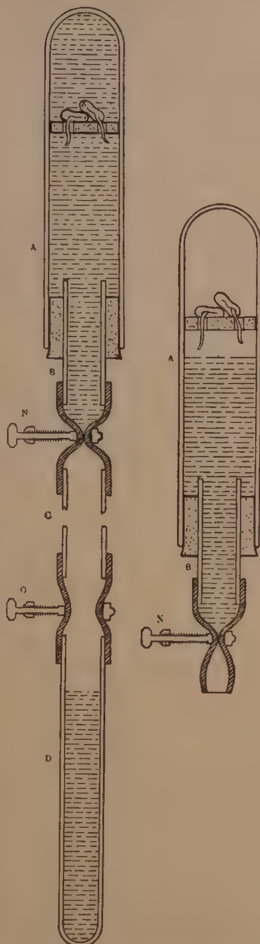

FIG. 75. Oxygen and growth.

control flask (containing killed seed) which would indicate contamination, necessitating the close of the experiment. Plot curves of the temperature conditions in the two flasks.

Oxygen and growth. — After introducing seeds (Fig. 75) attached to a cork into A (shown at the left), fill AB with water recently boiled and recooled. Close stop-cock N, invert, connect with C (a tube with air only) and with D (a tube containing potassium pyrogallate (see p. 221). Shake the series (stopcock O open) until the oxygen is absorbed, close O, immerse vertically the OD end of the series into boiled, cool water, disconnecting D, and opening O temporarily, to relieve (by inflow of water) the negative tension due to the absorption of oxygen. Close O, remove the apparatus from the water, open N, permitting the oxygen-free air to escape into A displacing water. Then close N, detach the parts below the latter, and place the AB part (as shown at the right) under temperature conditions favorable for growth. Compare at intervals the growth with seeds similarly placed in an open tube.

Fermentation of sugars. — Properly fill two fermentation tubes (preferably the Kühne form) with a 10 per cent sugar solution (fresh) of each of the following: glucose, sucrose, and lactose. In each tube insert a fragment of pressed yeast, plug the mouth lightly with cotton, and in 24 hours or more compare the production of gas caught in the closed arm. Insert in those showing gas a stick of caustic potash and explain the results.

For experiments such as the above, continued so short a time, it is unnecessary to supply mineral nutrients, nor are sterilization precautions necessary.

Alcoholic fermentation. — Prepare 500 cc. of a modified Pasteur solution to contain the following: —

Glucose	75 grams
Ammonium tartrate	5 grams
Potassium di-hydrogen phosphate	1 gram
Calcium chlorid	.5 gram
Magnesium sulfate	.5 gram
Water	500 cc.

Pour this into a 1-liter Erlenmeyer flask and add 2 grams of pressed yeast. Fit the flask with a cork through which passes the short arm of a piece of glass tubing bent so that the long arm may reach over through the cork of a wash bottle containing baryta water. Do not connect with the baryta water, however, until there is time for the air in the flask to have been driven out by the gas which is being produced. (How may this be determined, approximately?) Describe the result.

When the fermentation is practically complete, or after one week, the flask containing the fermented solution may be connected with a condenser and distilled. At a temperature of from 80–85° C. redistill, and when a few cc. have been caught note the odor; then pour into a test-tube, add a crystal of iodine, heat gently to 60° C., and maintain at this temperature while adding a strong solution of caustic soda until the iodine dissolves. A yellow precipitate of iodoform is indicative of the presence of alcohol.

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Texts. *Barnes, Detmer, Ganong, Jost, Pfeffer.*

CHAPTER XIII

GROWTH

A PROPER conception of growth and important growth relations is fundamental in plant production. Growth necessarily receives consideration at least indirectly throughout every chapter, for it enters into any discussion of the relation of the plant to factors of environment; to the making, use, and accumulation of food-materials; and to the phenomenon of reproduction as well. In general, the practical measure of growth is yield. It is important, however, to examine somewhat more carefully certain observations and fundamental facts regarding the mechanism of growth.

175. The factors. — Growth is conditioned by internal and external factors. Among the internal factors must be assumed vitality, not explainable, yet known as an attribute of the living mechanism; heredity, operating to reproduce specific form; and often a certain food-supply. The external factors are many of the environmental conditions previously enumerated (section 5); and essential are moisture, a certain range of temperature, a source of oxygen, the several nutrients and crude food-materials, and (for continued growth in green plants) light. These factors in relation to growth and development receive special consideration as independent topics.

Klebs has in recent years developed important relations between the continuance of growth and certain external factors. For a few plants he has indicated the conditions tending to maintain vegetative growth and he has con-

Fig. 76. Effect of conditions on the growth of pine needles: the short needles were produced during the season of transplanting (poor water-supply).

trasted these with the influences inducing flowering — tending toward maturity. These are subsequently referred to (section 225), but it is important here to note that most plants exhibit such complex relations as to render the problem especially difficult.

176. Evidences of growth. — Observed as a whole the growth of any crop from seed-sowing to harvest is an obvious phenomenon. In general, the popular conception of growth in flowering plants is that conspicuous

Fig. 77. The effect of complex factors on the growth of corn.

form of increase in size and weight which may be noted as the seedling develops into the mature plant, as the rapid exfoliation of leaves, or as the unfolding of the flower-cluster. Growth is associated with the formation and extension of living cells, and it may result in pronounced changes in external form or in internal structure.

Growth involves at least two distinct phases. The one is increase in length, and often in size — extension; the

other is a change in internal structure, either within the cell, or affecting groups of cells, resulting in differentiation. Extension is evident, and differentiation may be obscure; when the flower is fully open, for example, growth processes may go on within, which may or may not result in evident increase in size or weight, but new and important structures may be formed, and there is growth. Just so there is no

Fig. 78. A potato sprouting in a dry, hot atmosphere, and in strong light.

increase in the size of the incubating hen's egg, but by growth the little chick is soon developed from the simple fertile egg cell, with its stored food-material.

177. Growth of the embryo. — Growth of the embryo (Fig. 79) in plants has been nowhere more carefully studied than in certain of the crucifers, notably in *Capsella Bursa-Pastoris*, a classical example among dicotyledons, which

also may be taken as a type. After fertilization there is developed a row or filament of cells, called the proembryo, invested at the beginning, as a rule, with the endosperm. The apical cell of the proembryo divides longitudinally, and there are then cross and longitudinal divisions, either occurring first, thus producing a stage with 8 cells of the embryo proper, the remaining filamentous portion being designated suspensor. The following complete description of the embryonic growth from Coulter and Chamberlain[1] indicates the differentiation of the important regions of the young plant.

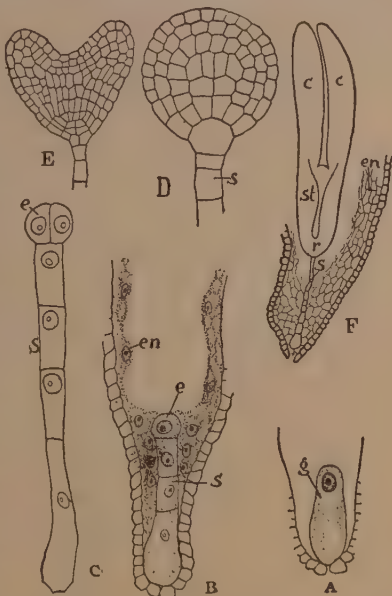

FIG. 79. Germination of zygote and embryology of Lepidium: fertilized egg (*A*); proembryo (*B*) with suspensor (*S*) and apical embryo cell (*e*); later stages (*C*, *D*, *E*, *F*) showing development of stem, root, and cotyledonary parts. [After Curtis.]

"Whether the transverse division precedes or follows the second longitudinal division, it separates the cotyledonary and

[1] Coulter and Chamberlain, "Morphology of Angiosperms," pp. 196–198.

hypocotyledonary regions of the embryo. In the octant stage the dermatogen begins to be differentiated, the periclinal divisions appearing first in the terminal octants and proceeding toward the root end of the embryo. The differentiation, however, is almost simultaneous, so that the dermatogen is soon completed, except that of the root-tip, which is derived from the adjacent cell of the suspensor, and appears comparatively late. The periblem and plerome are differentiated early from the tissue within the dermatogen. The stem-tip and cotyledons are derived from the four apical octants, and the bulk of the hypocotyl from the four basal octants. The root-tip, however, is completed by the adjacent cell of the suspensor. This cell divides transversely, the basal daughter-cell taking no part in the formation of the embryo, but the other daughter-cell (hypophysis of Hanstein) filling out the periblem and dermatogen of the root-tip. The hypophysis divides transversely, the daughter-cell next the embryo completing the periblem of the root. The other daughter-cell by two longitudinal divisions gives rise to a plate of four cells, each of which divides transversely, the plate of four cells toward the embryo completing the dermatogen of the root-tip, and the other plate constituting the first layer of the root-cap."

178. Polarity. — This term denotes a differentiation of the two poles of a growing cell or organ. Any part of any seed-plant or member is therefore recognized as having an apical pole and a basal pole, the apical being the direction of growth of the shoot, and the basal the direction of growth of the root. From the preceding description of the growth and differentiation of the embryo the sig-

nificance of this phenomenon may be seen. Polarity is known merely through the behavior of organs.

179. Elongation of roots. — The nature and distribution of the tissues at the apex of the root axis have been noted. The elongation of the root may be readily followed by a simple experiment. The tip of a young seedling should be divided into zones by a half dozen or more parallel marks about 2 to 3 mm. (about $\frac{1}{10}$ inch) apart, the first mark, however, being practically at the tip. The marks can be made with India ink and a pen, or a very fine brush.

Observations after from 6 to 24 hours, under favorable conditions, will show that the region of elongation is confined to a space covering usually only a few millimeters back of the tip. The zone farthest away may have already ceased to elongate, or practically so; while those nearest the tip elongate at first slowly, then faster, to a maximum, after which they decline. In fact, if new zones were constantly marked off each would be seen to go through a certain grand period of growth. The importance of the shortness of this region of growth with respect to the ability of the root to penetrate the soil has been pointed out in the discussion of the relation of the root to water and to the soil (section 30).

New lateral roots form in the quiescent region behind the root-tip; such lateral roots originate in the pericycle, just within the endodermis, and as they push out they literally break through the cortical tissues, which latter are in part broken down and dissolved. Lateral roots are, therefore, said to arise endogenously.

The growth and branching of the roots of agricultural

plants are in general increased by favorable food-supply and a water-content of the soil which shall not ordinarily be more than from 30 to 50 per cent of soil saturation, as discussed elsewhere. Under favorable conditions the rate of growth is rapid; for example, the roots of corn may elongate at the rate of about $1\frac{1}{2}$ inches per day. In many cases increase in size follows elongation, although it may be coincident with this.

Increase in the size of roots commonly involves no shortening of the root-axis, yet in the rooting of certain bulbs, and following the germination of a few seed, shortening may occur after the roots are fairly fixed in the soil, thus resulting in effectively burying or sinking the storage organ. The practical advantage is evident.

180. The stem apex. — The stem apex of the flowering plant shows, like the root apex, no single apical cell from which growth proceeds; instead, there is within the epidermis a group of cells rather indefinite in area which constitute the primary meristem. In the apical cells of this meristem divisions rapidly occur, and there is also a rapid extension of those somewhat older, or farther from the tip. This multiplication and elongation of cells is the direct cause of the observed increments of growth. The epidermal layer in order to accommodate this increase in growth is extended by divisions perpendicular to the surface (anticlinal divisions).

The cells of the meristem are gradually differentiated posteriorly in two chief regions, — an outer, or periblem, and an inner, plerome. It is primarily within the plerome that vascular tissue in seed-plants is differentiated (section 186).

The rate of growth extension in seedlings or other small plants may be conveniently recorded by means of auxanometers of various forms. A desirable type of this instrument produces a record by the following principle: A cord attached to the growing organ passes over a small wheel to a weight which takes up the slack induced by growth. The rotation of the small wheel carries with it a larger wheel from which a cord is connected with a pointer working against carbonized paper on a revolving drum. In this manner a continuous record is secured of the increments of growth.

181. The formation and exfoliation of leaves. — Originating in the developing periblem just behind the apex the young leaves arise, in spiral order, or verticillately disposed about the stem. These are at first small protuberances resulting from cell divisions parallel to the surface (periclinal divisions); but in time they flatten and grow faster than the stem apex. They curve over the stem apex more or less to form a bud.

In many annuals, and in perennial herbs, but only occasionally in trees, the leafy axis continues to elongate throughout the so-called growing season. If the shoot apex thus constantly elongates, each leaf in succession remains a part of the bud for only a short space of time, since by further growth, — more rapid on the upper surface, — complete exfoliation is soon effected. The exact point of origin of the leaf back of the stem apex depends in general upon the type of leaf arrangement in the species of plant. In the axil of each young leaf there is commonly formed later a region of growth destined to become a lateral bud. This bud also originates ordinarily

in the periblem in a manner very similar to the fundament of the leaf.

182. The resting bud. — Aside from the method of more or less continuous leaf development in the bud which has been stated to be the rule during the growth period of annuals, it is necessary to consider more particularly this phenomenon with respect to certain trees. In a majority of trees the shoot axis is terminated during the summer or early autumn by a resting bud. This bud is merely a very short leaf axis protected by bud scales, the latter being structures homologous with leaves or leaf parts. As a matter of fact, this terminal bud may be more or less completely differentiated in the early portion of the summer, but it does not necessarily present the appearance of a resting bud until midsummer or later.

Growth within the so-called resting bud proceeds very slowly, or may entirely cease, for several months during the winter. The following spring, with the return of favorable conditions for growth, there is generally a rapid unfolding of the leafy shoot, or of the cluster of leaves or flowers. It must not be understood, however, that this resting bud cannot be forced into more or less immediate growth, or that it is necessarily formed so early in the season. As a matter of fact, it appears that adventitious buds may arise and develop shoots during a single season, and that water shoots may form no terminal bud until completing a season of growth more or less equivalent to that of an annual.

183. Types of stem elongation. — Wholly apart from the exceptional cases referred to, the method of elongation of the shoot, or bud axis, in woody plants is diverse, and

the several types given below should not be regarded as clearly distinguished one from another: —

(1) Growth of the bud into a shoot may consist of the

FIG. 80. Stages in the elongation of a shoot of pine.

rapid elongation of the parts which have been previously laid down in the bud. In this case, the leaves which appear on the leafy shoot are merely the full number which

existed as leaves in minute form in the winter bud. Recent studies by Miss Moore indicate that a considerable number of our north temperate deciduous trees are of this type; and a number of observations suggest that it is the method common among conifers. Excellent examples of this type are offered by the beech and pine. In the beech the first sign of activity in the spring is that of gradual swelling of the bud, and at first a rather general stretching of the internodes. The bud quickly doubles its former length, and by this time observations upon the method of elongation are most easily made. It will be found that the growth increments in the basal internodes are at first stronger, successively passing to others, and the terminal internodes are the last to show rapid extension. Nevertheless, there is a distinct grand period of growth for each internode in turn.

In the pine, on the other hand, there is this difference: the shoot is unsegmented, and every portion of the bud axis from base to apex becomes successively the region of greatest extension; although in this case extension is more nearly uniform throughout the whole shoot axis. It appears that pomaceous fruits ordinarily follow the plan of this general type, but peaches may frequently fall into the next class.

(2) From the data available it would seem that the lilac, willow, and some other trees may develop normally during the summer a few more leaves than are ordinarily contained in the resting bud. In this case there is, of course, a formation of new nodes and internodes from the young meristem as the bud is expanded, or at least during the grand period of growth of the shoot.

It is quite possible that many trees show types of development from the resting bud dependent upon the conditions. In the Carolina poplar the writer has found that old trees may show an exfoliation of few if any more leaves than are normally contained in the bud, while younger trees in rapid growth may produce more than five times as many as were thus preformed.

Frequently the leaves of the apple, pear, peach, and other fruits seem to be produced in clusters upon short branches or spurs; in those cases, as a rule, the internodes are suppressed, and the axis is therefore greatly shortened. This is particularly common on fruit spurs. It is impossible here to consider the modifications in growth accompanying fruit production, the alternations of growth, elongation, fruiting,[1] etc.

184. Fruit buds and age of shoot. — It is of importance to consider briefly the relation of fruit buds to the age of the wood in a few economic plants. In the grape, the fruit is borne on canes produced during the current year. Where a vine is left for a season unpruned, many buds upon each cane push into new shoots, yet relatively few of these will then bear fruit, or at least, large bunches of fruit. As a rule, the better fruit-producing canes on American grapes are developed from side canes (pruned to a bud or two) on a leader which is not less than two years old.

Peaches and almonds develop fruit on wood which is one year old, and generally the fruit buds are more abun-

[1] For extensive observations on branches, fruit spurs, and other matters of interest in this connection, the student should refer to Bailey's "Lessons with Plants," pp. 1–69.

dant toward the middle portion of the shoot. On the other hand, apples are produced on wood which is two years old, and the same is true of cherries and plums. The pear belongs, in general, to the apple class, but on old spurs the relations may be somewhat more complex. It is evident, therefore, that the pruning practices with respect to any particular fruit must take into consideration not merely the effects upon general growth and form of the tree, but must consider also a proper regulation of the buds, shoots, or branches which are to produce fruit.

185. Persistence of the rest period in temperate regions. — Owing to the periodic production of the terminal bud, the shedding of the leaves, and the passage of the plant into a definite state of rest each autumn, it has been more or less assumed that this period is essential, and that it may only with great difficulty be shortened. It has been felt, particularly, that it is extremely difficult to force perennials into new growth before their normal resting period is completed. Klebs has shown, however, that under favorable conditions for growth, a number of plants require no winter rest period, and may be cultivated more or less continuously.

More recently, Howard and others have demonstrated that, even with those plants which are most persistent in refusing to grow until the normal rest period is over, etherization or other special forcing may be effective in giving the necessary stimulus to early growth (as developed later, section 197). First, however, it is necessary to indicate the effect of restoring, during the resting period, favorable conditions for growth. It is shown that of 234 species of plants brought into the greenhouses at

Halle, Germany, from October 28 to November 4, more than one half, or 125 species, began to make growth promptly under greenhouse conditions. Thus it is apparent that a large number of deciduous trees merely require favorable conditions for growth in order greatly to reduce the normal rest period.

Observation upon orchard and forest trees fully confirms this view. It happens frequently in temperate regions visited by drought in the early summer that the resting bud is formed early, and defoliation of many of the spring leaves may occur by midsummer. In such cases, a return of moist weather and favorable conditions in the late summer or early fall may result in a flush of growth from the resting bud of the same season. Sometimes this may be accompanied by fall blossoming.

186. Differentiation of stem tissues. — A complete study of internal anatomy, or histology, is not the purpose of the following paragraphs. It is, however, essential to note the common method of growth or development of some of the chief tissues and tissue systems within the plerome of the growing tip. There are produced by division and differentiation of the tip meristem strands of elongated cells known as the procambium.

In dicotyledons, these strands may be commonly 4 to 10; typically they are disposed as an interrupted ring in the outer portion of the plerome, surrounded by cells of a less differentiated meristem, often termed the ground or fundamental tissue. The procambial strands become by differentiation the primary fibrovascular bundles. In developing the common type of bundle (collateral type), the inner portion of the procambium becomes the

xylem, or wood, in which wood-cells, pitted and spiral vessels occur. The outer portion develops the phloëm, or sieve-tube and soft-bast part of the bundle. Between these two there remains a growing meristem, the cambium, which is most important in secondary growth, or thickening, as subsequently stated. In woody plants this cambium becomes a continuous ring, being formed between the bundles by the differentiation of the ground meristem.

In the root, however, the procambial areas originating the phloëm and the xylem of the several bundles alternate radially (radial arrangement); and when a ring of cambium is formed, it is between phloëm and xylem, as well as on the periphery of the xylem, thus constituting an irregular or lobulate ring.

187. Secondary thickening.—Secondary vascular growth normally arises by the development of new bundles from the ring of cambium. Ultimately so many of these secondary bundles may be interposed as to produce in woody or semi-woody plants a complete wood-cylinder. The bundles may be more or less completely separated one from the other by thin bands of ground-tissue, known as medullary rays. In perennials, the cambium differentiates each year (or season) new xylem within; thus the cambium is carried farther and farther from the center. It develops new phloëm without, so that both wood and bark are annually or seasonally augmented. However, the xylem vessels produced during the first flush of growth, that is, in the season of greatest activity, are larger and more important, and they have thinner walls than those produced later, so that a definite ring formation results.

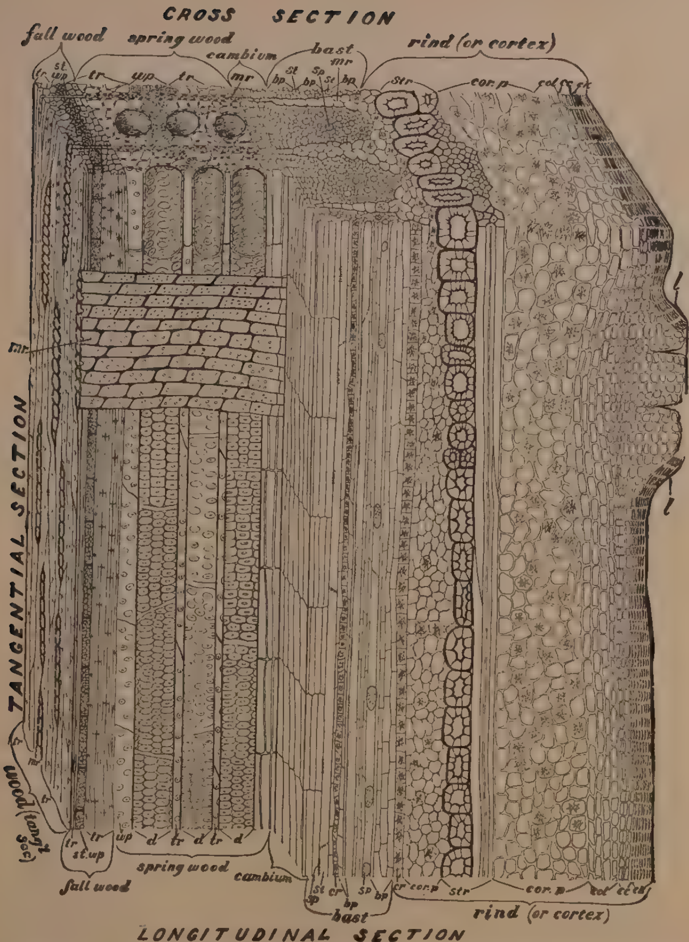

FIG. 81. Oak branch in cross, tangential, and longitudinal section: cork (*ck*), cork cambium (*cc*), parenchyma (*cor. p.*), stereome (*str*), bast (*bp*), sieve-plate (*sp*), sieve-tube (*st*), duct (*d*), tracheid (*tr*), wood parenchyma (*wp*), medullary ray (*mr*), and lenticel (*l*). [After Osterhout.]

Y

In a monocotyledon, like the Indian corn, the procambial strands are rather numerous, and generally irregularly disposed. The differentiation of this tissue into the mature elements is also complete, so that there remains no growing tissue in the bundle, and there is no further growth by secondary thickening. The thickening in the stem which results between the young and mature stages of the corn is very largely due to an increase of the size of cells already laid down at an early stage.

The leaves of many dicotyledons are generally more or less completely formed with respect to fundamental tissue very shortly after they begin to unfold, although there may be a subsequent growth and differentiation in the veins and veinlets. On the other hand, in the case of certain monocotyledons, especially, a growing zone, generally indefinite in extent, may be maintained for a considerable time near the base of the leaf. A few plants, such as the ferns, also elongate for a time by growth at, or near, the apex.

188. Growth of the cell. — It has been abundantly indicated that the growth of the organs of the plant, and of the plant as a whole, are dependent upon the capacity of the meristem or embryonic cells to extend or to divide. Extension is commonly associated with differentiation and maturity. It may result in a great relative reduction of the protoplasmic content, or as previously shown, it may result in protoplasmic loss, and eventually in the death of the cell, the firm cell-wall alone remaining. This type of cell growth, therefore, usually produces a specialized tissue, and the differentiation is to some extent an immediate growth response, for the extent of

these tissues may be determined, in considerable measure, by the conditions of growth.

Many meristematic cells, especially cells of the pri-

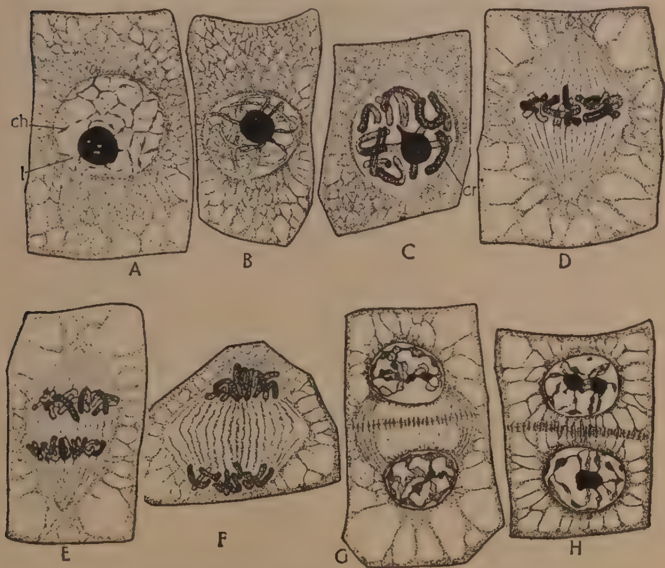

FIG. 82. Nuclear and cell division in the root of corn: cell with prominent resting nucleus (*A*); prophases of nuclear division, spirem (*B*) and chromosome (*C*) stages; bipolar spindle (*D*); early (*E*) and late (*F*) anaphases; telophases (*G*) and first evidence of cell-plate; location of cell-wall clearly defined (*H*). [After Curtis.]

mordial meristem, are so situated and conditioned that growth or increase of the protoplasmic content takes place, and at the same time the size of the cell may increase; this condition, however brought about, usually results in cell division.

189. Cell division. — Usually, in vegetative organs, division results in such manner that any meristematic cell, temporarily regarded as a primary (or often designated parent) cell, produces two more or less equal secondary (daughter) cells. Exceptionally, differentiation may accompany division; and, in any case, the subsequent life history of the secondary cells may or may not be similar. It is obvious that cell division must carry with it the division of most of the essential organs of the cell. There is, in fact, division of nucleus, cytoplasm, and plastids. The nuclear division is of peculiar interest.

190. Nuclear division. — The nuclei of both plants and animals seldom divide by a direct halving of the nuclear substance, or direct division. Such a type of division is, however, known. The usual process is complex, characterized by several distinct phases, all of which are apparently important in securing the equal division of certain chromosomes, or nuclear segments, which appear during division. This indirect process is termed mitosis, or karyokinesis. The observation of nuclear division usually requires material which has been carefully fixed (with respect to protoplasmic structure), sectioned, and stained.

A meristematic cell from the root of Indian corn may typify the usual phenomena (Fig. 82). During the growth of the cell, the nucleus exhibits toward certain stains definite reactions, and these are, for the most part, greatly intensified during division. The nuclear reticulum shows at first some small chromatic thickenings or scattered areas taking the stain more deeply, whilst the nucleolus is also deeply stained. When the reticulum-

like nature of the nuclear substance gradually gives way to elongate chromatic structures, or to a chromatic band, the prophase of the nuclear division is well advanced.

Later there appear well-defined nuclear segments, termed chromosomes, these resulting apparently from the aggregation and growth of chromatic substance in a certain area. Coincidently, the nucleolus is less stainable and may show an apparent degeneration, foretelling its final disappearance. The chromosomes thicken, the nuclear membrane disappears, and out of the mass of fibrous protoplasmic elements now present, there is oriented first a multipolar, and later a bipolar, spindle with the chromosomes arranged as an equatorial plate. In this stage, the metaphase, spindle fibers are attached to either side of each chromosome, and a longitudinal split is apparent. The halves of each chromosome separate and the "daughter" groups move (anaphase) to opposite poles of the cell, where the organization of the daughter nuclei proceeds (telophase). Here a new reticulum is ultimately evolved and a nucleolus reappears, formed, doubtless, in some manner from the nuclear material. Upon the remaining spindle fibers at the middle points thickenings occur, and these gradually extend as a plate between the two "daughter" cells. Thus the cell-space and the cytoplasm also are divided, and the cell division is complete.

Upon the reappearance of the chromosomes in every successive mitotic vegetative division, the number of these segments is constant; that is to say, there is a definite chromosome number for every species of plant, and the same is true of animals.

191. Cell division and respiration. — It is obvious that the growth of the embryonic cell in protoplasm often leads to a climax of energy-release in the complex activities of nuclear and cell division. When growth of the cell does not lead to division, or multiplication of kind, it is usually a progression towards differentiation, a process likewise involving abundant metabolic changes and energy-release. It is not strange that respiration in healthy organs is, in general, a measure of growth intensity.

192. The relation of pruning to growth. — Pruning, as applied to trees, shrubs, and vines, is a practice which has as its chief ends a regulation of growth and fruiting, and a shaping or training of plants. Either one or the other of these ends may be purely incidental, but the process is most important as a thinning of the fruit buds, and for the regulation and distribution of new wood. The practice must vary with the species of plant, and with the local ideas of proper size and shape. Properly performed, it is physiologically rational, and the world-wide development of the practice attests its effectiveness. Pruning should not be regarded usually as a special form of forcing for fruit production.

In trees the leaf buds often develop most abundantly at the tips; that is, at the periphery of the entire tree, so that the tree grows as a constantly enlarging shell. There are many more buds produced on the periphery than could possibly be developed profitably. Ordinarily, many more begin to develop than could succeed. Pruning is needed to suppress some buds, and to permit others to grow more vigorously. It is also needed with certain fruits in order to cut out and restrict large branches, so that light may

enter the central portion of the tree, for the encouragement of fruit production throughout.

In the majority of cases, cutting out some of the old wood or pruning off a portion of the young wood, incites more vigorous growth in the parts remaining. A too heavy pruning may be distinctly injurious. It may incite a large sucker or water-shoot growth at the expense of

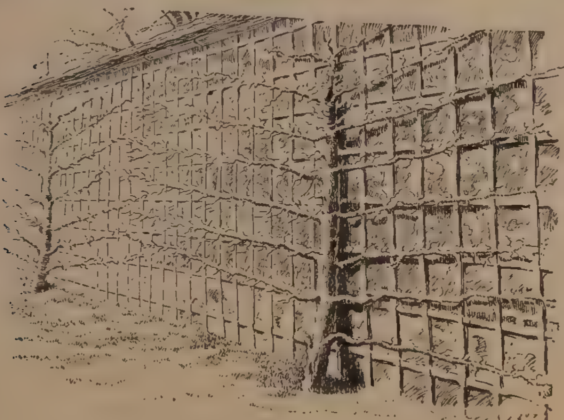

Fig. 83. Pear trees trained against a wall.

fruiting, produce a general weakening of the tree, especially by loss of organic food to the roots, and finally become a source of danger through the unnecessary wounds. In general, pruning is most common in order to maintain a certain balance between vegetative growth and fruiting. No plant can illustrate this relationship better than the grape. A failure to prune during a single season will be followed by the development of a large number of

canes, but the bunches of fruit will be small and poorly filled.

Pruning at the time of transplanting is invariably necessary in order to keep the balance between root and shoot. Resetting or transplanting may result not only in injury to the roots, but often in the death of all rootlets;

Fig. 84. The healing of wounds, after cutting off a lateral branch; first formation of callus (*cl*), after which three seasons (rings) of growth were required. [After Curtis.]

and while the latter are being developed the leaf surface must be reduced.

Ordinarily, pruning is a late winter practice, and this is desirable, in the first place, because there is no injury from bleeding, and secondly, on account of the prompt covering of wounds by growth in the spring. For the latter reason, also, branches are cut close to the main branch or stem, where practicable, and no large stubs are left.

The covering or healing of wounds by the growth of tissues beginning about the margin of the wound is a

response or adjustment bringing with it most important sanitary advantages. A wound long exposed is an almost certain beginning of a heart-rot of some type. The development of tissue covering the wound proceeds from the cambium. A callus or cushion of vigorous meristematic tissue is produced, and this is extended from all sides, until the wound is completely closed, when new wood-rings are laid down over it (Fig. 84).

193. Budding and grafting. — The growth processes immediately involved in budding and grafting are well understood, but all of the relations of stock and scion are not so clearly defined. In both budding and grafting, the important principle is to unite the cambium of stock and scion. When held firmly in contact by grafting-wax or raffia, the meristems of the two individuals thus united develop a callus, effecting a close union; and wood is subsequently laid down from each contributing part, cementing this union completely. In general, a union so close as to insure the life of the scion is only possible when the plants are closely related. If stock and scion grow at a different rate, that is, if the seasonal rings of one are thicker than those of the other, there will be a considerable difference in size

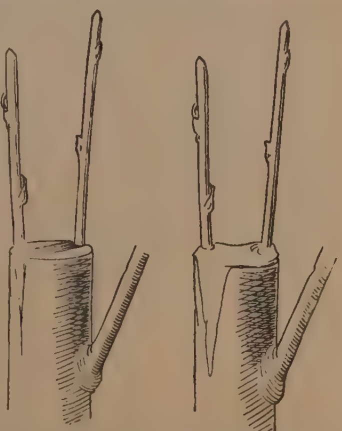

Fig. 85. Grafting: cambium of stock and of scion (on one side) in contact.

of trunk above and below the region of the graft, and this difference becomes more pronounced with age. Improper, or difficult, union, if it does not result in immediate death, will inhibit the transfer of material between shoot and root, and may lead to an abnormal swelling in the region of the union.

194. Scion propagation. — As referred to in the discussion of reproduction, vegetative propagation is often desirable, and propagation by buds or scions possesses a variety of advantages, some of the most important of which are as follows: (1) for the maintenance of varietal characters, especially when the plant is of uncertain or hybrid origin, when a return to the seed would yield an unknown progeny, (2) for the more rapid propagation of desirable species and varieties, and (3) for certain advantages of growth or hardiness which may result by placing the scion on roots other than its own.

195. Relation of stock to scion. — Commonly there is believed to be relatively little direct formative influence of the stock upon the scion, and an analysis of the facts thus far demonstrated makes it clear that, as a whole, the relations between stock and scion are very complex. The effect of the stock upon the total amount of growth is most evident in dwarf varieties, such varieties of the pear, for example, are obtained by grafting pear scions upon quince stocks. The scion is then furnished, in all probability, by a root system less active in absorption, and the effects of this are evident not only in diminished size, but also in slight modifications of leaves and sometimes of fruit. Waugh has called attention to certain differences in vigor of growth as well as in size and serration of leaves

caused by the use of different stocks with plums. The *Milton* plum worked on *Mariana* stock is more vigorous,

FIG. 86. Fasciated shoot of Fritillaria, apparently induced by rapid forcing.

and develops larger leaves than when *Wayland* or *americana* stocks are employed. In the former case, however, the leaf serrations are finer.

In the case of some other fruits, greater hardiness or resistance to cold is secured by grafting upon hardy stocks. The sweet orange is now commonly grafted upon the rough lemon and upon the sour orange, both in Florida and California, although some believe that the quality of the orange is thereby somewhat affected. Several species of American grapes are notably resistant to Phylloxera (especially *Vitis rotundifolia* and *V. riparia*), and these vines are now commonly employed as stocks in certain sections of southern Europe where this insect has done great damage. Since the insect is mainly injurious upon the root, there is a direct advantage in using American stocks.

The transmission of certain diseases, or pathological conditions, such as peach yellows, contagious chlorosis, etc., may occur by grafting, but in general it is felt that there is relatively little of what may be termed special chemical influence of the stock upon the scion. Literature is full, however, of contradictions and strife regarding the mutual influence of stock and scion. An hereditary effect has been claimed, but the lack of definite work with strains sufficiently pure, renders the whole matter problematical.

196. Forcing. — This term is rather loosely employed. It may signify merely the production of plants out of season, generally under glass or other protection, such as the growing of tomatoes in the winter; again, it may suggest the growing of plants which, in a particular latitude, require certain well-controlled conditions. These applications of the term require no further consideration physiologically. When, however, it is implied that forc-

FIG. 87. Leaves of rhubarb grown under diverse conditions: in the open (A); forced in dark cellar after being frozen outside (B); forced in well-lighted cellar (C).

ing involves production under abnormal, or what may be termed intensified, conditions, that is, under conditions stimulating rapid growth, then factors may enter in which require special attention from the standpoint of growth-stimulation. High temperature, increased moisture, and an abundant food-supply are the factors commonly involved in forcing. Under such conditions there is, of course, up to a certain maximum, a stimulation of vegetation. High succulence and brittleness are characteristics of forced crops.

For the production of salad crops, radishes, etc., forcing may be continuous, while in other cases, forcing conditions are employed to start resting plants or roots into rapid and vigorous growth for early market, as in the case of roots of rhubarb and asparagus brought in from the open. Large roots of rhubarb grown in the open for three of four years may be lifted in the late winter or early spring, reset in loose soil in a special cellar, hot bed, or greenhouse, and then forced into rapid leaf-stalk production. Forcing may also be employed for bulbs, tubers, and seed in the seed bed. The practice in general requires special care with ventilation; it often demands subirrigation, and it repays a constant watchfulness with respect to sanitary surroundings. Otherwise, the conditions may greatly encourage the growth and spread of fungous diseases and the development of other pathological disturbances.

A special phase of forcing has become important in recent times. This consists in awakening activity in dormant plants or organs by means of warm water or anæsthetics.

197. Etherization. — Etherization of plants and bulbs is rapidly becoming a common forcing practice with florists, and it is to some extent applicable in market garden work. By means of a suitable incubation in an atmosphere of ether or chloroform, it is possible to furnish the incitation for rapid growth, particularly in the case of resting plants and dormant bulbs and roots. It is thus possible to bring such plants into more rapid vegetation and flowering, to meet the special demands of particular seasons or occasions.

Stimulated by the many experiments of Johannsen, in northern Europe the practice has been very successfully employed in forcing lilacs for the cut-flower trade, while in southern Europe it is usually applied to the "mimosa," a species of Acacia. It is notably economical of time, space, and heat, in forcing many bulbous flowering plants.

In general, a common method of etherization is as follows: The plants are exposed from 24 to 48 hours in a tight chamber or box to an atmosphere of ether vapor, with an ether tension preferably from 30 to 40 grams per 100 liters of space (approximately $\frac{1}{3}$ ounce per cubic foot). The concentration and the length of exposure should, however, vary to suit the material, the more delicate material requiring the weaker treatment. After treatment the plants are ordinarily placed immediately under conditions favorable for growth.

If employed relatively early during the period of winter rest with the lilacs, marked contrast is shown between the forced and the control plants. During the early winter, in the latitude of New York, this plant can be brought into flower after etherization in from three to six weeks,

whereas twice as much time would be required without etherization. Later in the season the lilac is not so readily forced, and there is no such marked contrast between the treated and the control plants. Material

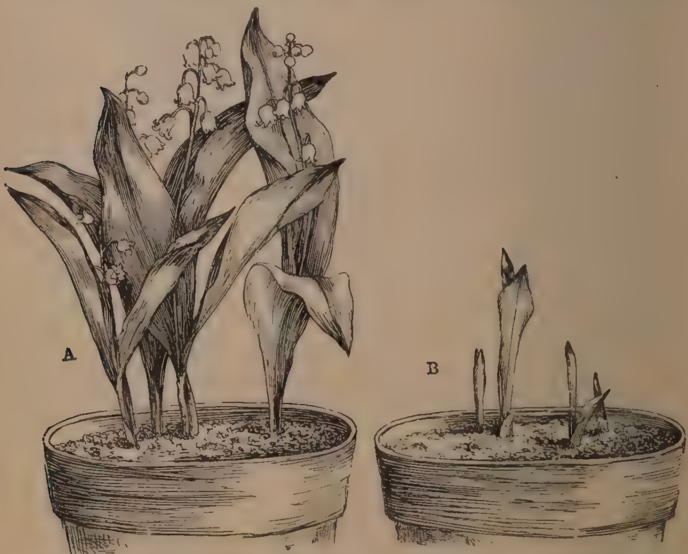

FIG. 88. Lilies of the valley, etherized (*A*) and unetherized (*B*), then grown under similar conditions for the same length of time.

capable of beginning growth immediately cannot be forced in this way.

There is some contradictory evidence respecting the etherization of bulbs, but in general, the practice has been successfully employed with lilies of the valley, narcissus and daffodils, and certain lilies and tulips; but the best

results in the United States have been obtained with lilies of the valley. In many cases, the treated bulbs have been brought into perfect blossom two or three weeks earlier than normal.

Howard determined that etherization will incite to more rapid bud activity a large number of common deciduous trees. He employed in one interesting series of experiments. shoots from 70 species of trees, including many

Experiments with 70 Species of Trees and Shrubs

Treatment	Time in Days to begin Growth	Time in Days to fully open Buds	Per Cent which grew	Per Cent whose Buds unfolded completely
Control	21.5	28.1	58.5	44.2
Etherized 48 hours	13.1	20.3	62.8	50.0
Etherized 48 + 48 hours[1]	12.7	18.3	47.1	35.7
Dried 1 day	20.7	26.2	52.8	45.7
Dried 5 days	13.8	18.7	35.7	32.8
Frozen 8 days	18.3	23.8	47.1	22.8
Frozen 14 days	16.4	23.8	14.2	11.4
Darkness 8 days	22.8	29.1	55.4	34.2
Darkness 14 days	23.9	29.2	58.5	32.8
Frozen 8 days, Etherized 48 hours	11.5	15.5	31.4	15.7
Frozen 8 days, Etherized 72 hours	9.9	16.4	30.0	21.4
Frozen 8 days, Darkness 5 days	17.5	25.0	21.1	20.0
Darkness 8 days, Etherized 48 hours	20.5	26.5	65.7	38.5
Darkness 8 days, Etherized 72 hours	18.2	25.8	48.5	35.7

[1] Interrupted exposure.

species which are known to be difficult to force into activity. In this test there were employed several species of Acer, Alnus, Azalea, Castanea, Cornus, Cratægus, Fraxinus, Populus, Quercus, Tilia, and Ulmus, besides many genera represented by a single species. Shoots from these plants were brought into the greenhouse at Halle, Germany, from December 8 to 23. The preceding table indicates the result of the etherization processes, and also compares this method of forcing with others involving change of conditions.

198. The effect of etherization. — There are as yet no such definite indications as will permit a competent explanation of the effects of etherization upon the plant. By some the treatment is assumed to cause a stimulation, and no further suggestion is made. The view is also advanced that there is an indirect effect upon the stored food. Again it is assumed that there is a loss of water from the cells, equivalent to a considerable time factor in the general maturity process. There is apparently no experimental work to confirm this view, and no ordinary method of desiccation is so promptly effective. It is more probable that the permeability of the protoplasm is directly influenced.

199. Forcing by immersion in warm water. — In order to start into more rapid and certain growth dormant stock for transplanting, it has long been the custom with some gardeners to immerse the roots in warm water. Recently Molisch has reported many interesting experiments based upon a practice of forcing by means of warm water. The method is applicable to most plants commonly etherized, such as lilac, mimosa, Forsythia, and bulbs. He has

also found it possible to force in a similar way several hardy shrubs.

The method consists, in general, in immersing the plant

Fig. 89. Shoot of lilac: branches to the right forced by the hot-water method of Molisch; branches to the left, control.

or branch in water at a temperature of from 30 to 35° C. for a period of from 9 to 12 hours. When potted plants are employed, it is preferable to invert the pot and immerse the stem portion only, since the roots are generally more sensitive to injury. This method has certain practical advantages over etherization, and if as generally successful, it will doubtless become important. The changes brought about by this treatment have not been determined.

200. Transplanting after wilting. — Practical truck growers are often met who are in the habit of wilting certain seedlings before transplanting, claiming that plants thus wilted recover promptly and grow off more vigorously than others not so treated. Experiment seems to confirm the practice for the tomato, and it may be suggested, provisionally, that the effect is indirect. A rather rough removal of tomato seedling from the seed bed results in some injury to the rootlets and root-hairs. If wilted, these roots do not recover upon transplantation, and vigorous new roots are promptly developed under suitable conditions.

On the other hand, it appears that in the case of those seedlings placed without wilting under more favorable conditions for growth, the injured roots may recover slowly, and generally new roots are not so promptly developed. It may, perhaps, be inferred that any plants which do not readily develop new roots, such as the lettuce, corn, etc., would be greatly injured by the wilting process. It seems certain that transplanting with so great a ball of earth as not to injure the rootlets would be preferable in all cases, except where the roots are so much entangled as

to require being set free. It is not at all evident why wilting may be favorable to many cuttings, unless, perhaps, there is a tendency to permit too many leaves to remain on the cuttings, the vigorous activity of which is then permanently checked or inhibited by the wilting.

201. Growth movements. — Growth movements of the varied sorts known may be referred to two types. These are (1) autonomic, or those resulting from internal and generally unknown conditions, and (2) paratonic, resulting as a response to external conditions or stimuli. Such movements are discussed in the special chapter on growth movements, also in those chapters dealing with the relations of plants to single environmental factors. It is sufficient here to note that there are various types of growth movement.

LABORATORY WORK

Elongation of root and shoot. — Determine the growing region of roots of the horse bean, bean, or field pea. Use germinating seed in which the radicle has developed to the extent of from 1 to $1\frac{1}{2}$ inches. With a fine thread dipped in India ink mark off parallel lines at equidistant intervals, of from 1 to 2 mm., placing the first mark in one or two cases as near the root-tip as possible and in other specimens at a full interval from the tip. Make daily observations and measurements and give a table or plot curve of the results. In order that the marked seedlings may be kept under suitable conditions, place each in the bell of a thistle tube (containing a little moist moss) with the root extending into the tube, the lower end of the latter resting in water. Favorable conditions may also be secured by pinning the seed, with the roots projecting vertically, to the bottom of a large cork to which has also been fastened moist filter or blotting paper. The cork is then fitted into a tumbler containing some water.

Mark off also convenient (about 2 mm.) intervals on several of the younger internodes of plants of Phaseolus growing in soil and determine the region of elongation of the stem. Determine also the total growth in successive internodes of a mature plant and develop a graph of the results.

Remove carefully the leaves from a node or two of half-grown oats or rye, mark off parallel lines on the internodes both near the basal and the upper parts, and describe the elongation phenomena, preserving the plants, if possible, under moist con-

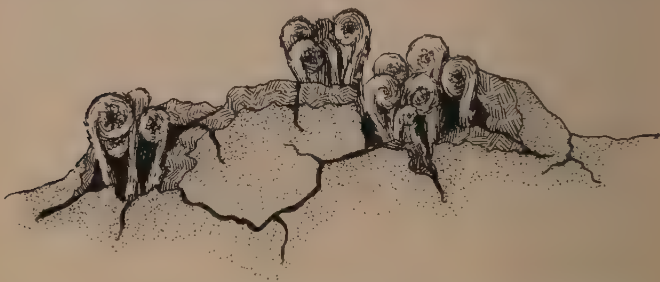

FIG. 90. Force of growth in the ostrich fern ; leaves breaking through concrete pavement. [After Stone.]

ditions. Study and prepare a curve of growth for the scape of dandelion, using plants growing either in the field or under greenhouse conditions.

Extension of leaves. — Study the rate of development of broad leaves such as those of grape, squash, or bean, measuring on successive days or periods both length and breadth.

Secure branches of one or more trees in winter condition, such as lilac, beech, poplar, and apple. Determine the average number of nodes produced by a season's growth and compare this with the number of nodes or leaves found by the dissection of half a dozen buds.

Growth in tissues. — Dissect out the growing point of Elodea or Hippuris, mount in water under a cover glass, and examine.

Describe the formation of leaves. From prepared slides study and draw the growing tip in longitudinal section.

From hand sections or from prepared slides study the secondary thickening in the stem of sunflower, castor-bean, or other plant of similar texture. Make some sections near the apex of the growing shoot and some farther distant in order to follow the development of inter-fascicular cambium and secondary bundles. From prepared slides measure the extent of variation in the growth of the seasonal rings.

Adventitious organs. — (Roots.) Follow the development of adventitious roots upon cuttings of tomato, geranium, or grape. In the case of tomatoes in fairly dry soil this is also conveniently studied by binding to the stem at a node a ball of moist moss. Germinate sunflower seeds and as soon as the radicle has emerged about $\frac{1}{2}$ inch cut off the latter about $\frac{1}{5}$ inch from the cotyledons, place the cotyledonary portions on moss in a moist chamber, and note the method of origin of the roots.

(Buds.) Grow seedlings of flax in a saucer of sand or soil until the hypocotyls have about reached full growth. Then cut off the upper portion of the plant about $\frac{1}{5}$ inch below the cotyledons and discard the leafy portion. Cover the rooted hypocotyls with a bell glass or tumbler to prevent drying out and follow and describe the development of buds. Study the fleshy root of sweet potato to ascertain if preformed buds are present. Halve the root, place it upon moist sand under a bell glass, and observe the development of shoots. Examine the leaves of *Bryophyllum calycinum* for the presence of buds in the indentations of the margin. If no buds are found, place the leaves on moist sand and observe occasionally. Follow likewise the development of buds from a leaf of *Begonia Rex*, placing the leaf upon moist sand with the petiole or a small part of the leaf slightly covered. Sever a few of the larger veins, and protect the leaf from drying out.

Hot water forcing. — During early winter or midwinter immerse for from 6 to 12 hours twigs of lilac (generally good) and apple in a water bath controlled at a temperature of 35° C. Reserve some twigs untreated, or immerse them in water at 20° for

control. Plan both sets under conditions favorable for growth, and compare the time periods required for development. It should be remembered that positive results are obtained by such

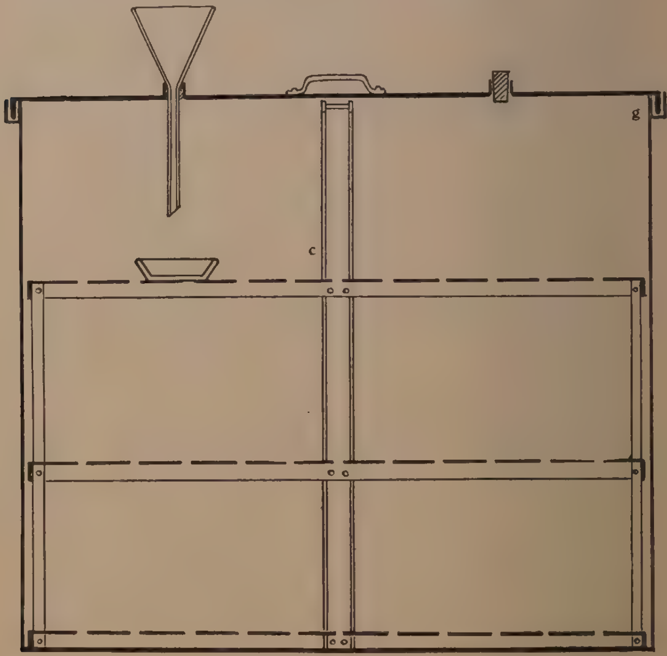

Fig. 91. A convenient etherization chamber, sectional view, showing also carrier (*c*), groove for melted paraffin (*g*), and method of introducing ether.

forcing only when the plants treated are not in condition normally to show immediate growth. Potted plants may be inverted and immersed to the edge of the pot.

Etherization. — In a tight zinc box such as shown in Fig. 91,

or in a chamber improvised from vessels at hand, etherize shoots or small plants of lilac and resting bulbs of lily-of-the-valley. Use about 40 grams of ether per 100 liters of space, and leave the plants in the chamber about 24 hours. Then place the plants with some untreated specimens under conditions favorable for growth, and compare the results. Write a short report stating your opinion of the extent to which such forcing may find practical application.

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TEXTS. *Barnes, Detmer, Ganong, Jost, Pfeffer, Stevens, Strasburger.*

CHAPTER XIV

REPRODUCTION

The production of new individuals by any method whatsoever is reproduction in the broader sense. Physiologically it is a complex and peculiarly interesting process. In the higher plants, — angiosperms and gymnosperms, — we are concerned with reproduction by seeds and reproduction by vegetative parts.

Seeds are embryonic plants with a certain food-supply and protective coverings, while vegetative parts may be shoots or any portion of the old individual which, when placed under favorable conditions, will develop shoot and root. The one type is usually sexual; the other is invariably nonsexual.

Vegetative reproduction generally implies (1) the adventitious development of roots, as in cuttings, bulbs, the potato, etc., where buds are preformed; or (2) of both root and bud, as in the sweet-potato, Dahlia, etc. Reproduction by seeds involves commonly a variety of phenomena including the differentiation of new structures, the fusion of cells (gametes), and the origination of a new individual from a fertilized egg-cell.

202. The seed habit and vegetative reproduction. — Reflection upon the general conditions prevailing among cultivated and wild plants leads to the conclusion that the

Fig. 92. Apricot blossoms; growth from stored food.

production of seed is for most plants of paramount importance. Vegetative methods of reproduction may also occur in plants possessed of the power of abundant seed production; and, indeed, under favorable circumstances the former may propagate individuals more rapidly. Supplementary vegetative methods of reproduction are therefore common. Wild onions and lilies may have their "sets" and bulbs. Numerous plants develop offshoots, root shoots, and natural layers, and so perpetuate themselves in a variety of ways. A few plants both wild and cultivated, such as forms of the water weed and the yam, have entirely or practically lost the power of seed-making. In general, however, the seed is the basis of plant production, although vegetative reproduction has been employed far beyond its natural course, and this in order to perpetuate a type, to multiply individuals quickly, and to grow plants under climatic conditions rendering seeding unprofitable or impossible.

203. The flower: essential structures. — Richness of color or striking form and fragrance in flowers may serve useful ends leading toward reproduction. Moreover, in ornamental plants these qualities often represent the crop value of the plant. Beneath an apple tree in spring the ground may be white, strewn with discarded petals, representing much energy of growth, that was, nevertheless, serviceable. In seed production, however, it is stamens and pistils which are directly important, and the inconspicuous, unobtrusive, or unattractive flowers of spinach, lettuce, and corn are as effective as the beautiful or gaudy structures of the orchid and hollyhock.

Fig. 93. Flower of barley.

204. Pistil and stamen. — The pistil is commonly composed of one or more carpels. Whether consisting of one or of several carpels, it embraces in common types (1) the ovule-sac, generally a membranous or fleshy structure, containing at the time of flowering the relatively small, seed-like ovules, or megasporangia; (2) a more or less well defined style, upon the terminal portion or surface of which is differentiated (3) the stigma.

The stamens consist in general of a stalk part or filament, supporting the anther, which latter contains the anther sacs, or microsporangia, with their pollen-grains. Stamens and pistil may be present in the same flower,

known as a perfect flower, of which the apple, cotton, wheat, etc., are examples. These structures may occur in different flowers, termed staminate and pistillate flowers, upon the same plant, that is, monœcious (one household) plants, of which the corn and squash are examples; but they may occur upon different individuals, that is, staminate and pistillate, or diœcious (two households) plants, of which latter type the hemp, certain

FIG. 94. Carpels and stigmas (*A*) of orchard grass; also enlarged view of stigmatic cells and pollen germination.

mulberries, and the date-palm are examples. In any case, approximately at the time the flowers are open, or mature, the anthers of healthy stamens may set free considerable pollen. At about the same time the stigma or stigmatic surface of the carpel is receptive; that is, generally, in a condition to catch or affix pollen-grains, and to afford special conditions for their germination.

205. Pollination and pollen-tube penetration. — Pollination is a mechanical process. As it naturally occurs, it

is the mere dusting of the stigmatic surfaces with pollen. This pollen may be derived from the anthers of the same blossom, from different flowers, individuals, or species.

FIG. 95. Flowers of date-palm : staminate cluster (*A*) and blossoms (*a*) ; pistillate cluster (*B*) and blossoms (*b*). [After Swingle.]

If such pollen-grains do not germinate, or if no germ-tubes penetrate the stigma, they may awaken no more response than so much dust. If we may acknowledge faith in the current belief regarding pollen as a factor in "hay fever,"

then the pollen grains of the ragweed, of timothy, and of some other plants are among those forms which may

FIG. 96. Staminate and pistillate blossoms of Begonia.

as dust, or perhaps in some chemical manner, severely irritate the mucous membranes of man. However, the

dusting of flowers with pollen would not be dignified with a name unless it led toward fertilization and reproduction.

The stigmatic surfaces of the receptive flowers are generally moist, and often provided with a perceptible

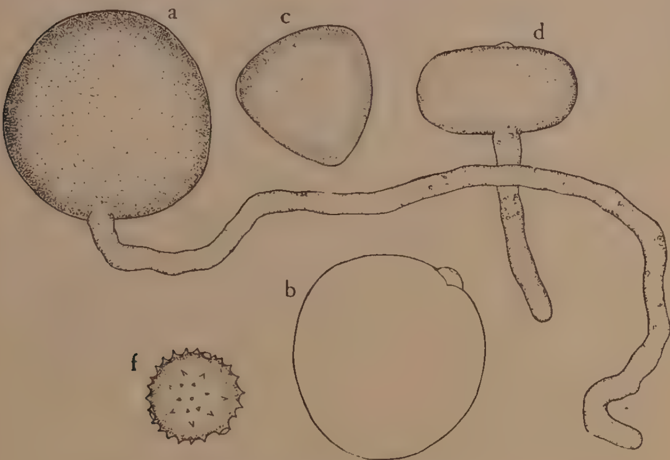

FIG. 97. Pollen grains and pollen germination; corn (*a*, *b*), apple (*c*), sweet-pea (*d*), and Althæa (*f*).

secretion. Upon this surface the pollen may germinate, — almost any pollen may germinate; yet it usually happens, from a variety of circumstances, that the pollen most abundant upon any stigma is the pollen of the same species. This is really what is generally implied by effective pollination. Strasburger, however, has made the interesting discovery that upon any particular stigma pollen of a plant in an entirely different family may not only germinate, but may even penetrate the style to some extent.

Normal pollination takes place through the agency of wind and insects, for the most part; and it may be interfered with by rain or other climatic conditions not resulting in the death of the flower. Such conditions may close the flowers, preventing the transfer of pollen; or beating rains

FIG. 98. Pistillate blossom of squash, showing large stigmatic surfaces.

may wash the pollen from the stigma. In consequence, orchards may fail to be productive through the effect of climatic conditions upon pollination.

206. Fertilization. — Fertilization is the union and fusion of two single gametic cells, or nuclei, which have previously been differentiated by a special course of development. In flowering plants the one gamete is derived

from the pollen-grain, the other from the embryo-sac in the ovule. In the fusion of these nuclei, usually derived from different organisms or flowers, the characters of two individuals are fused. Two lines of ancestry are brought together in one cell, the fertilized egg, or zygote, which will develop into the embryo of the seed. It is important to bear in mind some further details regarding the fertilization process.

The pollen, as has been noted, is a distinct phase of the plant. It represents upon germination the complete male gametophyte, whose reproductive function is the production of a gamete. In most cases the pollen-grain consists of merely two cells,—a smaller cell practically within a larger. The larger produces through germination a vegetative tube, the germ tube, which (in angiosperms) grows through a differentiated portion of the style, or stylar canal; thence it penetrates the ovule, commonly through the micropyle, until it comes in contact with the egg-apparatus, and ultimately with the egg-cell. The smaller cell of the pollen-grain is largely nucleus. The latter divides by the time the pollen-tube breaks or ruptures, and one of these two gametic nuclei fuses with the nucleus of the egg-cell, the other gamete; thus fertilization is effected. The fertilized egg — this single cell, or zygote — is the beginning of the new individual that is developed within the protecting coats of the ovule (now the young seed), in turn inclosed by the ovule-sac, and often by other parts of the flower which may assist in the development of the fruit.

207. Universality of fertilization. — It is remarkable how universal is this phenomenon of fertilization. It

occurs throughout nearly all the phyla and classes of organisms, and is of unquestioned importance. It is not possible to consider the many interesting opinions regard-

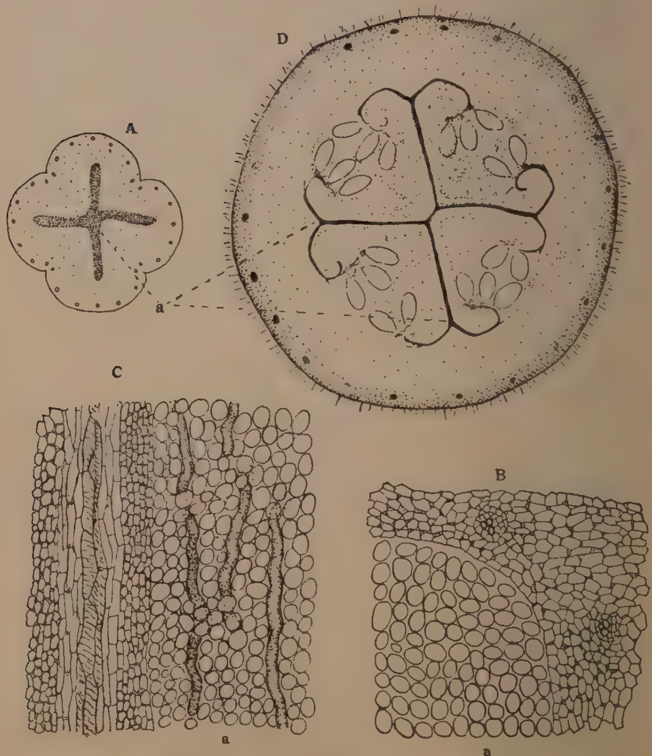

FIG. 99. Pistil of squash: cross-section of style (*A*), with region of pollen-tube penetration (*a*); portion of preceding, enlarged (*B*); longitudinal section (*C*) corresponding to the preceding; cross-section of ovule case (*D*) with region of pollen-tube penetration (*a*).

ing the results and benefits of the process; but emphasis should be laid upon the union of characters — amphimixis — thus effected. Reference is made later to the segregation of characters which is conceded to take place.

Every ovule requires a pollen-grain and a pollen-tube. In fact, for fertilization of all the ovules in any plant, many more pollen-grains germinate and penetrate the style, since two or more tubes may be directed toward the same ovule. The watermelon may develop more than five hundred seed, so that more than a thousand pollen grains should fall upon a single stigma to insure the maturity of all the seed.

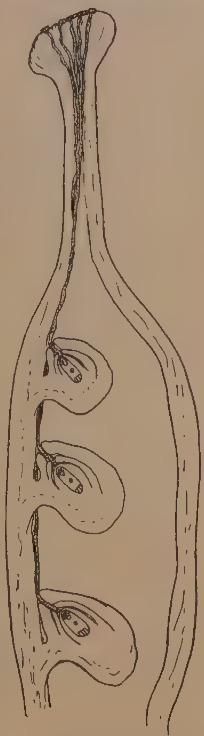

Fig. 100. Carpel of a legume, diagrammatic section at the time of fertilization.

All the ovules may be fertilized, yet this does not guarantee fruit development of all. Frequently the plant would be unable to support the weight, or growth demands, resulting from the development of every fruit.

Unfertilized blossoms are usually the first to fall, but familiar examples are evident on every hand of wild and cultivated plants which shed many fertile blossoms. Correlative growth influences, which are little understood, or an unfavorable environment, may take heavy toll as the young fruit develops; so that at maturity only a small

percentage of the flowers may have completed their functions. According to Waite, apples in good season set no more than 5 per cent of fruit, and of this small percentage much is lost during fruit development. If we put this into figures, we find that 1000 apple blossoms may yield about 50 young fruits, of which only some few reach maturity. In other cases, practically every ovule may mature, if fertilization is effected. This is particularly true of plants producing fewer flowers or floral axes, as the corn or strawberry.

Fig. 101. Blossoms of cotton; showy, but often self-pollinated.

208. Cross-fertilization and self-fertilization. — These terms are used more or less loosely. Cross-fertilization generally indicates a fusion of gametes derived from different individuals, resulting, therefore, from pollination of a stigma with pollen derived from a different plant. To be consistent, self-fertilization would then indicate that both gametes are derived from the same individual.

As a matter of fact, there are several grades of self-fertilization; thus fertilization as a result of pollinating the stigma with pollen from the same blossom, from a different blossom upon the same plant, or from another plant derived by bud or scion propagation from the same "parent" stock. In much the same way cross-fertilization is a broad term, applying when the gametes are derived from any two individuals (grown from seed) within the species; that is, whether the crossing is between individuals from pure lines, from merely mixed seeds, or from distinctly different strains or races.

When reference is made merely to the dusting with pollen, the terms self and cross pollination should be employed, but many authors writing popularly fail to make these distinctions.

209. Cross-fertilization apparently the rule. — Cross-fertilization is a phenomenon of common occurrence with a considerable number of ecologically well-established native species of plants, and vigorous cultivated varieties as well. It is evidently effective, but it is by no means universal among seed-plants. If we accept the analysis which has thus far been made, it is, however, far the more common method among flowering plants. Cross-fertilization is, of course, dependent upon cross-pollination, and both are commonly associated with the remarkable developments in form, color, and other characteristics of numerous familiar flowers to which popular attention has been so much attracted. Nevertheless, it should not be understood that these striking peculiarities of floral structures are in strict correlation with cross-pollination. Dates, mulberries, hops, and hemp are invariably cross-

pollinated and cross-fertilized when fruit is produced, because in these species stamens and pistils are on distinct individuals. In corn there is opportunity for self-fer-

Fig. 102. An ear from an isolated stalk of corn ; infertility from lack of cross-pollination.

tilization, but crossing is the rule. In fact, isolated stalks of corn seldom set more than scattering grains (Fig. 102).

Darwin's observation respecting the necessity of cross-pollination in red clover has become a familiar instance among perfect flowers. He demonstrated that the heads of this species protected from bees and other insects set no seed. This may not be due, in the case of clover, to the ineffectiveness of the pollen of each particular blossom

upon the stigma of the same flower, but rather to structural difficulties preventing pollination; that is to say, it appears that the flowers may be self-fertile; nevertheless, the effect is that the best seed production requires insect visits. In consequence, to produce clover seed economically, this crop should be permitted to flower only in the season when the bumblebees are abundant and active. The first crop is too early, so that it is commonly cut for hay, and the second crop is permitted to develop seed.

210. Darwin's conclusions. — A study of the remarkable morphological devices in many flowers pollinated by insects suggested to Darwin the importance of determining, with respect to the offspring, the comparative physiological effects of cross and self fertilization. He made fertility and constitutional vigor of the offspring his field of investigation. As a result of his extensive experiments with some familiar plants throughout a period of years, Darwin concluded that "cross-fertilization is generally beneficial, and self-fertilization injurious." In drawing these conclusions, he made careful comparisons of the offspring with respect to height, weight, constitutional vigor, and fertility.

Darwin recognized some general exceptions, in which, for instance, self-fertilization was often more effective for a generation or two (as in tobacco and Petunia) than crossing with relatively closely related individuals. Nevertheless, in the case of tobacco a cross with wholly fresh stock was invariably more effective than self-fertilization. The most notable exception to his general statement, quoted above, occurred in a vigorous individual of the morning glory (*Ipomœa purpurea*), Hero, whose

descendants "varied from the common type, not only in acquiring great power of growth and increased fertility when subjected to self-fertilization, but in not profiting from a cross with a distinct stock; and this latter fact, if trustworthy, is a unique case, as far as I have observed in all my experiments."

211. The need of further work. — The question of cross and self fertilization (cross-breeding and in-breeding) is now receiving renewed attention. The indications are that with many plants in-breeding is for plant production far less dangerous than has been supposed. It seems to be conspicuously dangerous in the case of corn, some reasons for which will be subsequently considered. Shamel states, "In the breeding of tobacco it is well known that cross-pollination within the limits of a single strain produces inferior offspring, and only self-fertilization gives offspring of the highest degree of vigor, though hybrids between distinct strains of tobacco often display a vigor superior to that of either parental strain. Examples could be continued indefinitely, but even one instance, in which long-continued in-breeding results in no injurious effects, would be sufficient to discredit the old hypothesis."

It is evident that in breeding studies each crop must be examined with respect to this important point. It is to be expected that much new evidence on the general problems of self and cross fertilization will be available, for the more certain methods in recent years with pure-line ancestry, the conception of unit characters, the development of biometry — all make possible far more definite experimental conditions.

212. Experiments with self-sterility in pear. — Waite

established an important principle in fruit-growing when he showed that many varieties of the pear are self-sterile. In the case of some varieties the capacity to set fruit when self-pollinated is wholly lacking; in other cases when the varieties are limited to their own pollen, normal fruits may be developed, yet even then fruit production is con-

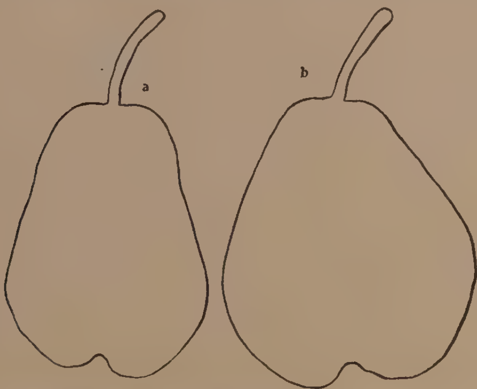

FIG. 103. Difference in size of pears self (*a*) and cross pollinated (*b*). [After Waite.]

sidered to be less certain and the size often slightly reduced. These results, and many others since reported by various observers, are particularly interesting, since self-pollination has reference not merely to the use of pollen from the same plant, but also from other individuals within the variety. We are dealing, in this case, with clonal varieties, such varieties being maintained by budding and grafting. Different individuals are looked upon, therefore, as very closely related. In most instances all are de-

scended from some one ancestral or stock individual, and there have been, so to speak, nothing but generations of this original individual. Pollination between the different trees in a block of Bartlett pears would, therefore, be considered self-pollination.

According to Waite, some of the common varieties of pear generally self-sterile are the following: Angou, Bartlett, Clairgeau, and many others, 22 in all. The varieties showing a capacity for self-fertilization were 14 in number; among these being the Flemish Beauty, Keiffer, Le Conte, and Seckel. Climatic conditions have been shown to be of some importance with respect to the general problem of self-sterility (cf. Fletcher).

213. Self-sterility in other orchard trees. — The apple, plum, peach, and other fruits are similarly more or less self-sterile. The investigation of self-sterility, which was given a special impetus through the work of Waite, has resulted in a modification in orchard-practices of immense economic value. It is certain that the grower needs to consider an adequate distribution of varieties so that pollination with effective pollen may be secured to all. A particular variety may not be constantly self-sterile under diverse conditions, and it is clear that many problems respecting pollination await careful investigation.

214. Parthenogenesis. — There are exceptions to the rule that the egg cell must be fertilized in order to develop the embryo of the seed. The maturation of a cell occupying the position of an egg with or without the usual segregation, or reduction, division and its development without fertilization constitute parthenogenesis. This phenomenon is reported to be characteristic of several forms of

dandelion; and there are similar instances among hawkweeds, meadow rue, Alchemilla, and several other genera of flowering plants. In fact, if we examine the cases reported for all plants, both higher and lower, we find that parthenogenesis, or that which is here included under that term, is not uncommon. Development without fertilization is a well-established phenomenon in certain insects and other lower animals. There are also some extremely interesting cases of what has been termed artificial parthenogenesis, reported by Loeb, Lefevre, and others. In the latter the artificial development of the egg-gamete, without fertilization, is induced by chemical or physical stimuli. When there is no tendency toward natural parthenogenesis, this artificial stimulation of development has never gone so far as to produce adult individuals, but larval stages have been successfully reared.

215. Xenia in corn. — The appearance of the seed gives usually no indication of the pollen which was effective in fertilization. In corn, however, the observation was recorded nearly two centuries ago that certain colored sorts planted together "will mix and interchange their colors"; that is, in the seed of the first year there will be mixed colors. Numerous carefully conducted experiments in recent years by De Vries, Correns, Webber, and others now clearly demonstrate the immediate effects of the pollen in corn, and a physiological explanation is at hand.

215a. Indications of xenia. — We may first note the results of xenia. If pollen of the black Mexican or Cuzco varieties, forms possessing a bluish-black aleurone layer, are applied to the silks of white or yellow sorts, many of the seed resulting show the blue-black color of the pollen

FIG. 104. Xenia in corn, showing the immediate effect, through double fertilization, of the pollen-producing parent. [Photograph from Bureau of Plant Industry.]

plant. Again, if the young ears of sweet corn are pollinated with a pollen from Dent and Flint varieties, there result many seeds with smooth kernels and starchy endosperm (Fig. 104). These results may be secured with pure-line strains under control conditions, and the phenomenon is recognized as xenia. Characters such as those above noted alone exhibit true xenia; thus color or chemical content, qualities which reside in the endosperm, are of this nature, while qualities evident through the embryo belong to another category. The explanation of this endosperm phenomenon has now been found in the process of double-fertilization.

Generally the nucleus and cytoplasm of the embryo-sac develop the endosperm, and only the pistil-bearing plant is concerned with the qualities of this material. In the lily, in corn, and in many other cases more recently made known, the nucleus of the embryo-sac may fuse with the second sperm nucleus from the pollen-tube, and thus the endosperm may acquire, as well as the embryo, qualities of the pollen-producing plant. It is evident that corn which possesses color by virtue of a pigment in the pericarp will not show this type of phenomenon, for the pericarp has no means of becoming immediately endowed with the qualities brought by the pollen. Cases of xenia, therefore, should not be confused with ordinary speckled ears. The latter may result in the second generation, or later, from crosses in which color is one of the characters of one or both parents, or from bud variation. Xenia is a question of physiological interest in plant production, but it has apparently very little practical bearing. When it exists, it is an infallible sign of hybridization, and in some cases

it may serve as a valuable control suggestion in hybridization work.

216. False xenia. — Certain beans and peas show externally in the color of the embryo the immediate effects of the pollen. The seed-coats are more or less colorless, and the characteristics of the embryo are, therefore, apparent. Physiologically this is in no way comparable to the previous phenomenon, and if the term "xenia" is used in this connection, it should be expressed false xenia.

217. Other secondary effects of pollination. — Under xenia we have considered only those instances of the subsidiary effects of the pollen which may be attributed directly to fertilization, or double fertilization, and manifest through effects produced in a readily explained manner upon the embryo and endosperm. A certain special stimulating action of pollination upon structures outside of the ovule was long ago suggested by Focke and others. The problem may, for the moment, be restricted to cases in which there is fertilization. The question may then be formulated as follows: In the normal production of fertile seeds, is there any evidence that pollen from different varieties or species will influence the form, color, or quality of the fruit?

Beyond all question, the form of the fruit, and even the quality of the fruit, will be affected when only a few ovules are fertilized; for the reason that there will be incomplete development of the fruit as a whole in the great majority of plants, notably in many varieties of the tomato and apple. Opinions differ regarding the important effect of pollen from different varieties on the form or color of fruit when fertilization is complete. In various horticultural

reports it has been stated that very often a definite effect is due to the source of the pollen. An analysis of the data seemed to indicate that the observations which have been made neither positively confirm nor deny a direct and specific stimulation of the pollen upon the fruit-production. In the paper previously referred to, Waite draws this conclusion: "There seemed to be, however, constant differences between the Bartlett fruits crossed with different kinds of pollen. If these distinctions can be confirmed by future experiments, a question of considerable importance will be settled." Lewis and Vincent seem to concur in the belief that there is an immediate effect of the pollen, and they cite the deep red color in Spitzenberg apples pollinated with Arkansas Black as compared with the lighter red obtained when Jonathan is the pollenizer.

218. Parthenocarpic development. — It is considered to be a general rule that lack of fertilization is followed by more or less prompt shedding of the infertile blossoms. There are, however, important exceptions to this course of development. Seedless fruits of garden and orchard crops are known. Seedlessness, or imperfect seed development, is very properly associated with the failure of fertilization, although it may happen that some ovules fail to develop after fertilization. On the whole, it seems to be clearly demonstrated that in some cases the ovary and attached parts, technically the fruit, may develop as a purely vegetative organ, varying more or less, of course, in size from its normal form when fertilization has taken place.

Among vegetables the cases of parthenocarpic development best known are those of the English forcing cucumber and certain varieties of the eggplant. Gardeners fre-

quently prevent the pollination of the forcing cucumber, especially when it is to be used for fancy market purposes. Certain varieties normally show the development of seeds toward the apical end of the fruit only, and this part is then more or less abnormal in size, so that the general form of the plant is injured. It would appear that in the case of the eggplant a relatively small number of blossoms will, under ordinary circumstances, develop fruit without seeds, and Munson succeeded in obtaining fruits of normal size and form. Many other observations might be cited of the occasional appearance of seedless vegetables, but our chief interest should be directed towards certain observations upon fruits.

219. Parthenocarpic formation in pomaceous fruits. — Waite ascertained that in certain cases self-fertilized pears " are deficient in seeds, usually having only abortive seeds, while the crosses are well supplied with sound seeds." In fact, there were two significant exceptions to the rule requiring pollination and fertilization for fruit development. Upon the Le Conte and Heathcoate varieties a few fruits were set without pollen. Still, in those two instances, there was some doubt as to the complete exclusion of pollination. A few isolated instances of the occurrence of pears, apples, and other pomaceous fruits without seed have been recorded, but the possibility of perfect fruit development in certain varieties, or the development of varieties which may not require fertilization, has only recently been carefully investigated. Ewert for one has made this matter a subject of experimental study, and it would appear that when pollination is prevented, perfect fruits may result in the Cellini and

Charlamowski apples, and in six varieties of pears, of which the most important is the Clairgeau. In the best of the cases reported by him the fruits suffered neither diminution in size nor change of quality, although parthenocarpic development is commonly accompanied by decreased size. Sections of well-fertilized and seedless fruits are shown in Figure 105.

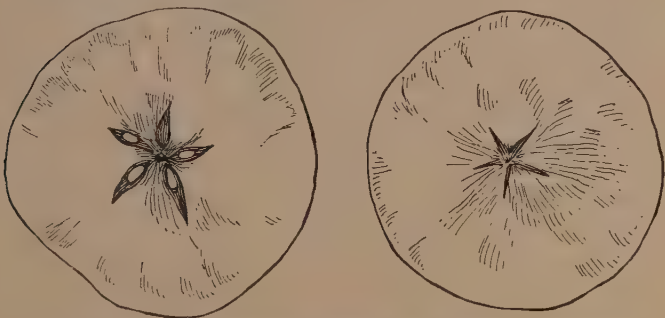

FIG. 105. Section of fertile (seed-bearing) and seedless (parthenocarpic) apples.

219a. Seedlessness in the orange, grape, and banana. — Well-established varieties of citrus fruits, commercially important, normally produce no seed. The California navel oranges are of this type. In this instance pollination cannot lead to fertilization, since, according to the reports available, the stigmatic surface apparently fails to reach full development, or to become normally exposed, and thus germination and the entrance of the pollen tubes is precluded. Further observations upon this point are needed.

Historically of more interest are certain cases of par-

thenocarpy among grapes. The small seedless black or currant grapes of Greece and the eastern Mediterranean region furnish the dried currants of commerce. Other instances are to be found in the famous Sultana and a few other raisins now propagated in California as well as in the Mediterranean region. The percentage of seedlessness in one of the table grapes, Black Eagle, is likewise considerable. The cause of seedlessness, or lack of fertilization, in these cases does not seem to have received scientific attention.


FIG. 106. Seedless navel (parthenocarpic) and common (seed-bearing) orange.

Many varieties of the banana fail to set seed, although it would seem that effective pollen is produced.

220. Nonsexual reproduction. — Multiplication by vegetative parts is notably common among plants, wild and cultivated. A single individual may in various ways give rise to a colony or complete plantation of its own kind without the production of seed. These may remain in organic connection for a period of time, or they may be promptly separated, one from another, by the death of connecting parts. Wheat and other cereals and grasses have the habit of stooling; that is, of multiplying by buds from the lower submerged nodes. Blue-grass and Johnson-grass are among those plants which produce underground stems, while the decumbent Bermuda and quack-grasses are among those which regularly take root at the joints. White-clover spreads in a way analogous to the latter, and the strawberry develops runners which bud

and take root a few inches or more from the parent plant. Advantage may be taken of all such nonsexual methods in practical propagation. Moreover, in all such cases the vegetative method enables the producer to be sure of the variety or form, the propagation of which he is continuing, since there is then, at least, no chance of mixing by hybridization, or of change through segregation. As a rule, plants that reproduce in a vegetative manner occupy the land quickly. The method is, of course, of great service when the plants are useful, but it may be most trying when this habit is that possessed by a persistent weed.

221. Thickened roots and tubers. — Irish potatoes and Madeira vines are types of plants propagated by tubers or thickened stems, produced generally only by underground buds. In the varieties of the potato commonly grown the seed-ball is now seldom seen, so that there are varieties the existence of which, in culture at least, is dependent upon vegetative reproduction. Sweet potatoes, yams, dahlias, and other familiar plants are propagated by thickened roots. Many of these forms have in cultivation, under ordinary conditions, lost the power of seed production. The propagation of some edible and many floricultural plants by bulbs and corms is so common among liliaceous genera that the production of bulbs now represents a group of special industries. Holland is famous the world over for this type of work, but doubtless the conditions there afforded are practically duplicated in many other places.

222. Cuttings. — A countless array of ornamental herbaceous forms and some small and bush fruits are regularly propagated by cuttings. In fact, carefully

handled, there are few herbaceous plants of indefinite growth which may not be successfully multiplied in this manner. In general, the growth relations are simple. The propagator employs a small portion of a branch containing one or more nodes. These nodes with active or dormant buds are capable of developing shoots. The essential response demanded of the plant is that under conditions favorable for growth it shall be able to develop adventitious roots. Such roots are by no means uncommon in nature, and they develop apparently more or less in correlation with the needs of the plant. The extent to which plant parts are able to develop such roots is remarkable. It has been ascertained that cotyledons and leaves are in no small number of cases able to develop these roots as efficiently as stems, and the leaves could, therefore, be employed in propagation if there were also the possibility of bud development. In fact, there are a few types which have the habit of producing buds, and such leaves are made use of in this manner. The leaves of several species of Begonia, notably the varieties of *Begonia Rex*, also certain forms of Bryophyllum and related plants, are thus employed, as already indicated.

223. Precautions with cuttings. — It is evident that branches or shoots used as cuttings require, in general, careful treatment. Twigs or canes in a resting condition may require no special consideration, so that currants, grapes, and other fruits root readily under field or garden conditions. Throughout the South, sugar cane is generally propagated by planting the whole stalks, and also by using the lower parts of stools, — the rattoons. Shoots in full leaf always require more attention, since the loss of

water (transpiration) may be excessive and death by drying-out is then a chief cause of failure. In all cases the reduction of the transpiratory surface to a minimum is required, and it is essential that the conditions of the cutting bench shall be most favorable with respect to moisture, drainage, light, and temperature. The exposed cut surfaces are also more subject to the attacks of hemi-parasitic or damping-off fungi; therefore, the cutting bench requires the same careful attention as the seed-bed. In many cases a thorough knowledge of the growth habits of the plants and the best skill of the gardener will be required to determine the conditions needed. It may be necessary by special means to induce root development in the portion to be used for a cutting before the branch is separated from the stalk, as by attaching a pot with moist soil or moss. Special cases, however, are too numerous to receive consideration.

224. Vegetative reproduction and running out. — Some observers have held that vegetative reproduction repeated through numerous generations results in deterioration; but many or all of the cases cited in substantiation of this view are, in the opinions of others, wholly invalid. Nevertheless, in one sense varieties may "run out." Thus bud variation may be so great that in time the original form may be entirely lost; this is "varying out."

It would seem that the yam (*Dioscorea sativa*) has been vegetatively propagated in China for two thousand years, and there is no evidence that it is decadent. The sweet-potato has apparently long lost the power of seed production, and we cannot assume that it has lost in vegetative vigor. The fig and the date have not been commonly

grown from seed for several centuries. The European grape-vine (*Vitis vinifera*) has been grown more than 5000 years, and vegetative propagation has been the rule. When native American vines were carried to Europe, diseases new to Europe were introduced, and European vines were so susceptible that enormous injury resulted. Many thought that this weakness with respect to disease was a result of the long vegetative culture; but this seemed to be disproved by the fact that seedling sorts of that species of vine were equally susceptible.

Resistance or susceptibility to any disease appears to be, in many cases, a character, or a complex of characters, and may follow known laws of heredity, as in the case of other characters subsequently discussed. Moreover, among the more familiar molds and other fungi there are some notably ubiquitous and vigorous forms which are not known to possess sexual stages. Among the species of living things generally, however, the frequency of gametic fusion, on the one hand, and the complete loss of this process among others constitutes a biological paradox.

225. Relation of vegetation to fruiting. — Plants exhibit a remarkable diversity in the relations between vegetative development and fruiting. With respect to annual, biennial, and perennial habits this has been briefly considered. Generally speaking, fruiting is the climax of a continuous or interrupted period of vegetative development. The American Agave grows many years vegetatively, and then through the formation of an enormous flower-stalk and abundant fruits the leafy parts are drawn upon to such extent that they are left exhausted and incapable of recovery.

Under exceptional conditions fruiting of the oak or apple may occur in the nursery stock. On the other hand annuals may be induced to grow for a period of years without flowering. With a careful selection of conditions, and by employing vegetative propagation when necessary, Klebs was able to induce continuous growth and fruiting in *Parietaria officinalis*. Uninterrupted growth, without flowering, was obtained with *Fragaria lucida*, *Glechoma hederacea*, *Rumex acetosa*, and other species, — plants which normally produce blossoms in summer. These facts suffice to suggest the complexity of the relations, and the importance of determining the releasing stimuli, with respect to vegetation and fruiting.

LABORATORY WORK

The flower. — Review or study the morphology of the flower, giving attention to monœcious and diœcious plants as well as to those with perfect flowers.

Study more completely the floral mechanism in two or three representatives of some one order, such as the Liliaceæ or Leguminosæ. [Consult Church or some other convenient text.]

Anther and pollen. — Cut crosswise the large anthers of some plant, such as lily or tomato, press out the pollen-forming areas, and note the changes in the character of the contents of the anther (pollen) sacs, or microsporangia as maturity proceeds.

Study and describe the pollen from plants in at least two different orders, mounting it both dry and in water.

Set up germination experiments with pollen from several plants which produce tubes readily (within a few hours) in water or sugar solution. Germinating well in 3 per cent sugar solution there are among the numerous monocotyledons which might be used, several species of lily, also orchids, tulip, and Narcissus; while cucumber, buttercups, willows, and Erica are among favorable dicotyledons.

The pollen grains may be sown in a drop of the sugar solution on the slide, which is then placed in a moist chamber. Preferably, however, prepare hanging drop cultures (Fig. 107) made of glass rings cemented to the slide with wax, over each of which is inverted a cover-glass with a drop of the solution, in which the grains are sown. In the bottom of the cell is placed the same solution as employed in germination, and upon the upper rim of the ring is a thin layer of petrolatum in order to afford a closed chamber.

Pollen of corn and some other grasses, also many sedges and rushes, germinate best in a moist atmosphere, and these may be sown on a dry cover-glass inverted over a cell containing water.

Fig. 107. Hanging-drop cultures, used in the study of pollen germination.

Pistil and fertilization. — Follow the changes in the stigmatic surfaces of several flowers as they open. Trace the canals or modified tissue through which the pollen tube penetrates. In the lily, squash, or cucumber, and many other plants the pollen tubes are readily seen in longitudinal section.

If prepared slides are available, study the morphological evidences of fertilization.

From the open buds of any plants convenient dissect out the stamens ("emasculate") before the pollen is matured, or the stigmatic surfaces exposed; inclose the flowers in paper bags, or oiled paper, and after a week or more determine the effect upon ovule development and seed production in comparison with control plants. With a diœcious plant, such as Indian corn, merely protect from pollination the pistillate axis or ear.

Fruit setting. — In the proper season make a careful count of the number of blossoms produced by such plants as the apple or peach, and later determine the percentage of fruit which may be set.

Xenia. — Examine ears of corn from plots in which a starchy dent variety has been grown alongside of, or together with, a sweet corn. In the case where sweet corn was planted note particularly the influence of the starchy variety in modifying endosperm characters, and compare this with the amount of modification in the other variety.

Parthenocarpy.— Examine the seedless fruits of any material available, such as banana, grape, navel orange. Determine the extent of ovular development. If English forcing cucumbers (such as the Telegraph) are available, cut out the stamens before the pollen is matured, bag the flower, and determine the effect upon the development of fruit in comparison with that of a fruit hand-pollinated at the proper time.

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CHAPTER XV

THE SEED IN PLANT PRODUCTION

NECESSARILY the quality and potential vigor of the seed are most important considerations in crop production. Quality is to a very large extent based upon physiological conditions. It does not seem entirely appropriate to discuss here such matters as "true to type" seed, impurities and adulterants, the contamination of the seed by means of fungous spores present, or of a dormant mycelium within the tissues which may carry disease to the new crop. We are concerned, however, with the adaptability of the strain to the conditions under which it is to be grown, and with the capacity of the seed to produce the most vigorous plants of which the variety is capable. Quality of the seed so far as vigor and adaptability are concerned will be affected by conditions which permit of an arrangement in the following category: —

By the conditions under which the parent plant has been grown.

By the conditions under which maturity has been attained.

By methods of harvesting and curing.

By the period and conditions of storage.

By size and weight.

226. Habitat conditions of the parent plant. — This is properly an hereditary consideration, but it is conven-

iently treated here for special emphasis. It is now established beyond reasonable doubt that the quality of seeds will be modified in a single generation by the climate and cultural conditions under which the crop has been grown. This may have no reference whatsoever to the special factors influencing curing, storage, and the like. For a long time it has been clearly recognized that if early corn, notably sweet corn, is grown from the same seed at points North and South, there will result differences in the quality of the seed produced, so far as earliness is concerned, so that if seed from the two regions are sown side by side, that from the North will mature earlier.

It is possible that in an indirect way the differences may be in some cases ultimately referred to maturity; yet these effects must be regarded, at present, as the immediate effects of the environment. Many data respecting the rapidity of the changes which may be induced under different cultural and climatic conditions have been given in agricultural literature. The table on page 340, from Lyon, exhibits results with a variety of wheat grown several years in different localities (with, of course, some opportunity for selection) and finally in adjacent plots in Nebraska, — these being strains which were, "without doubt, originally the same."

The facts developed regarding corn are also true when applied to spring wheat and oats, for it is agreed that in planting spring wheat, seed obtained from farther north will ripen earlier and give better yield, as well as quality, than seed of the same strain introduced from a point farther south. In the case of winter wheats, however, the facts seem thoroughly to substantiate the general belief

that the reverse condition is true; that is, seed from points south give a better yield than northern grown seed of that strain. In general, adjusted local varieties are best.

MODIFICATIONS INDUCED IN WHEAT BY ITS ENVIRONMENT

	KANSAS SEED	NEBRASKA SEED	IOWA SEED	OHIO SEED
Date of sowing	Sept. 9	Sept. 9	Sept. 9	Sept. 9
Lodged . . .	None	None	Badly	Badly
Rust . . .	Very little	Very little	Much	Much
Date of ripening . . .	June 25	June 27	July 2	July 3
Yield of grain per acre . .	29.1 bu.	27.5 bu.	22.3 bu.	23.1 bu.
Weight of grain per bushel .	64.2 lb.	62.2 lb.	56.9 lb.	58.9 lb.

227. Localization of seed production. — In many cases it is not possible to explain the localization which characterizes commercial seed production, and it would appear that seeds are grown in particular regions to-day, not only because of some apparent advantages of the region with respect to the maintenance or development of desirable hereditary qualities, but also because of such factors as (1) cheapness of production in the locality, (2) the effects of conditions upon maturity and curing, referred to later, or else (3) from merest accident. It would be well if more general recognition were given to the two underlying principles. On the one hand there are regions, or localities, especially favorable for the production of high quality in seeds; on the other hand, it is often the case that local seed production and seed selection would have

advantages outweighing all other considerations of special habitat.

In the United States alfalfa seed mature well only in the dry climate of states like Colorado and Utah. In the South the potato matures so early that a long season of storage, resulting in probable injury, would be required if home-grown tubers were used in planting.

Some growers have expressed the opinion that there is a marked physiological change more or less gradually developed in strains of onions or radishes repeatedly grown in certain sections of California. It is not possible at present to determine if other factors have been overlooked, but at any rate it is believed that seed from radishes which have been grown for successive years in California will, when planted in other sections of the country alongside of the home-grown or recently imported seed of the same strain, show clearly that the far western-grown product has undergone some marked change with respect to eastern conditions.

Similarly, onions grown from California seed are said to be different in keeping quality from those bulbs grown from seed produced in Michigan. This effect is said to assert itself even when the most stringent methods of selection are practiced. There is grave doubt if this is a general rule, and we may well believe that varieties may be developed which will not show this tendency.

The seed of cabbage, cauliflower, and some other crucifers were first grown extensively in this country upon Long Island, and the region became famous for the production of these crops. More recently it has been found that a similar favorable locality is the Puget Sound region. Growers are so sure of the wholesome effects of these

localities upon the product that one will frequently hear it stated that the failure to head properly is due to the fact that the seed was not grown in either of these regions.

Tomato seed are grown extensively in Michigan, and they have been successfully produced in many parts of the North and of the central West. On the other hand, the belief is prevalent that tomatoes grown from seed produced in the South rapidly deteriorate, and that in the course of a few years the well-established and highly prized varieties may revert to the common little-tomato type. Here again there are no statistical data indicating that these opinions have been formed as a result of any properly controlled experiments. It is, for instance, quite possible that by means of crossing between varieties, or by crossing with the little-tomato type these reversions may be accounted for.

Tracy has reported that beans are promptly modified by soil conditions, and that in general seed should be grown on the type of soil for which they are intended. It is, furthermore, an interesting fact that German and French growers importing seed are often careful respecting the climatic and soil conditions under which the seed are grown.

228. Maturity. — Quality may also be affected by the conditions which maintain just at the time the seed is maturing or during the state of maturity. Too much moisture at the time the seed is approaching this state precludes a proper gradual ripening, and the final effect is usually manifest in decreased vitality; that is, lessened capacity to germinate, and this is true even if the seed is subsequently dried and stored. The reduced vitality

may be connected with the conditions in which the food substances are stored in the seed, with the development of injurious substances which lead to undesirable transformations, or with the continuance of activity after the seed should have attained practically a dormant condition.

Moreover, immaturity has a tendency to lessen the keeping quality of most seeds, and many of the shrunken seeds upon the market, frequently met with in the case of alfalfas and clovers, are due to their immaturity at the time of harvesting. Apparently it is a general rule that the sooner immature seeds are sown the more vigorous will be the plants which they are able to produce. In other words, a gradual deterioration takes place in storage, but more promptly than in the case of well-matured seeds. Extensive experiments in determining the effect of maturity upon vitality as exhibited by germination tests were carried out by Hellriegel. In the case of rye the seeds were harvested at four different stages, and the following table indicates the relative condition of ripeness and the percentage of germination from such seeds, which were subsequently treated alike with respect to drying and storage: —

Stage of Ripeness	Percentage of Germination
Contents of kernel watery	4.5
Milk stage	5.0
Dough stage	9.5
Yellow ripe	36.0
Dry ripe	84.0

The above data were secured from seeds immediately separated from the parent stalk and then dried. When, however, the seeds were allowed to remain attached to the harvested stalks, notable gain in the vitality was shown by those seeds harvested in early stages. In such experiments as the last mentioned there is opportunity for considerable ripening after the early harvesting, and the results are not contrary to what might be expected.

According to the experience of some observers, a continued practice of selecting immature seeds may result in the development of an earlier variety. This is sometimes, however, at the expense of size, quality, and vitality.

Kedzie has shown the effect of maturity upon vitality of wheat, and his results are so striking that they may be presented in detail: —

MATURITY AS AFFECTING VITALITY (*Kedzie*)

DATE OF HARVEST	STAGE	YIELD PER ACRE	LENGTH OF PLUMULE
June 26	Milky juice . .	11 bu.	6.0 in.
July 4	Dough . . .	25 bu.	9.0 in.
July 10	Full yellow ripe	30 bu.	10.1 in.
July 12	Dead ripe . .	28 bu.	11.0 in.

It should be said, however, that so far as ability to grow is concerned, no very narrow restrictions may be placed upon the stage of development of the seed, provided adequate and suitable nourishment can be given the young embryo. In a series of experiments recently carried out by the writer, whereby the young embryos were transferred from the developing seeds to sterile nutrient solu-

tions, the results confirm the view that embryos thus treated are able to maintain themselves and sometimes able to develop mature plants. The vigor and strength of the plant, however, was in direct proportion to the degree of maturity of the transferred embryo. In view of these facts, it is unlikely that the selection of immature seeds is to be recommended as a means of securing earliness, unless, of course, all other methods fail.

229. Conditions of harvesting and curing. — The conditions of harvesting and curing form in a measure a continuation of the phenomenon of maturity, and a discussion of these factors might be included in a broad interpretation of the general process of maturity. However, it is a distinct phase of the subject and deserves full, independent consideration in this place. Uniformly favorable conditions for harvesting and curing a given crop, other factors remaining fairly similar, may alone be sufficient to establish seed production as an industry in a locality.

Among the most striking instances of localization which are to be found is that of the Santa Clara Valley, California. This region has won an enviable reputation for seed-growing, and over numerous other equally fertile localities it possesses the distinct advantage of relative certainty in the prevalence of uninterrupted dry conditions during late summer and far into the autumn, the time when most seeds are harvested. Hundreds of acres of the sweet-pea are grown for seed in California, yet the sweet-pea is equally thrifty and vigorous in many other sections of the country. Dry summers and autumns are particularly important, moreover, in cases where, in order to harvest the seed, the whole crop must be cut, and there results

consequently a large bulk of material which must be cured previous to threshing.

In harvesting and storing seed the unfortunate practice often prevails of storing the product in bulk; this in spite of the fact that no small proportion may be somewhat immature. As a common result, the material heats rapidly, and in the end much loss may occur (see section 168). This heating is due in many cases to respiration, yet a part of the difficulty also lies in the fact that the growth of microorganisms is much encouraged by the "sweating process."

230. Duration of vitality. — In recent years considerable attention has been bestowed upon the problems of maintenance of seed vitality, and upon a determination of the conditions which are injurious. Much new work and valuable data are therefore available; but the problem is not a new one, and much was done by De Candolle and others fully eighty years ago.

Species differ in a decided manner with respect to the length of time in which vitality is maintained, and this is true whether the conditions to which they are subjected are favorable or unfavorable. Among seeds readily killed by storage for a relatively short period may be included those of many Compositæ, Cruciferæ, and Gramineæ; while some of those far more resistant are Malvaceæ, Solanaceæ, hard-seeded Leguminosæ, and in general those with water or air-resistant seed-coats. It should not be understood, however, that all species of the same genus or family are even approximately alike in resistance. Becquerel reports an age of about eighty years for several species of legumes which were still capable of germination.

The following table from Duvel indicates the average loss of vitality of thirteen kinds of seed sent to seven different localities in the United States and to Porto Rico, and kept under ordinary conditions of storage, the first test covering a period averaging 128 days (February to June), the second period averaging 251 days (February to October): —

Kind of Seed	First Test	Second Test
	Deterioration in Vitality	Deterioration in Vitality
	Per cent	*Per cent*
Tomato	2.55	5.20
Pea	3.92	11.39
Corn, sweet "A"	1.20	12.17
Watermelon	.57	12.51
Lettuce	1.96	15.77
Radish	11.02	22.67
Corn, sweet "B"	12.47	26.10
Bean	5.76	29.58
Cabbage	7.22	43.56
Carrot	9.77	53.89
Onion	15.26	74.10
Pansy	38.33	84.90
Phlox Drummondii	34.97	85.85

The control seeds referred to in the table were kept in a cool, dry closet in the botanical laboratory, Ann Arbor, Mich., and these showed a remarkable vitality.

231. Environmental conditions. — Duvel determined that under ordinary conditions moisture and temperature are the more important factors. Rise of temperature alone may not be injurious unless accompanied by in-

creased moisture-content. The following table gives a record of vitality as related to precipitation and temperature at the seven points in the United States where the thirteen kinds of seed were stored: —

Place where Seeds were Stored	Average Loss of Vitality 13 Kinds of Seed	Annual Precipitation	Temperature	
			Mean Fahr.	Maximum Fahr.
	Per cent	*Inches*	*Degrees*	*Degrees*
Mobile, Ala.	71.98	91.18	71.4	96
Baton Rouge, La.	41.39	66.37	72.2	98
Durham, N.H.	39.58	48.20	52.3	98
Auburn, Ala.	33.91	62.61	64.4	98
Lake City, Fla.	29.38	49.76	73.3	103
Wagoner, Ind. Ter.	28.41	42.40	67.1	107
Ann Arbor, Mich.	2.52	28.58	49.12	98

In general, it would seem that a further drying out of thoroughly matured seeds may enhance the keeping capacity. Moreover, such mature seeds keep well at high temperatures. Immature seeds, or those which may not be thoroughly dried out, keep best in a cool, dry situation. When moisture is present, it would seem that respiration is rapid and may be regarded as an important factor in reducing vitality. Under ordinary conditions "the life of a seed is undoubtedly dependent on many factors, but the one important factor governing the longevity of good seed is dryness."

232. Buried seed. — Duvel, Beal, and others have shown that, in general, seeds which are buried deeply maintain their vitality for a long period. An instance

came to my attention in Columbia, Mo., of the germination of clover seed which had been buried for more than thirty years. The conditions were these: A cut was made in clay soil exposing the ground-level of a fill made more than thirty years before of from two to four feet. A few weeks after the exposure of the old ground-level a continuous growth of white clover appeared along that line. There could be no doubt of the age of those seed, and an examination of undisturbed soil farther in disclosed the fact that there were present not only white and red clover seed capable of germination, but also, in smaller quantity, cocklebur, sonchus, and a species of sedge.

In general, it would seem that the burial of agricultural seeds results in death far more promptly than in the case of resistant weed seeds. Shallow burial of weed seeds, however, affording moisture conditions favorable for decay, may often result in their destruction.

233. Delayed germination. — The rest period of the seed seems to be to a considerable extent, if not entirely, due to the development of a structure, or device, during the maturing process which may serve to exclude water or air until acted upon by gradual processes of decay or special agents. It is well known that the germination of many seeds is quickened by soaking in strong sulfuric acid, by cracking the tough seed-coats, and some even by the action of the digestive juices of certain animals.

Nobbe and others have pointed out the relation of germination to certain structural devices. Recently Crocker finds that the marked case of delayed germination in the seed of Abutilon is due to the fact that the condition of the seed-coats precludes the possibility of

water absorption. Again, in the case of a few seeds, it seems to be established that the exclusion of oxygen is the important factor. The resting spores of many fungi are notably difficult to germinate until after a period of rest, and it is quite probable that similar factors are concerned here, especially through the deposition of some resinous substance in the cell-wall.

234. Effect of weight and size of seed upon vigor. — Since the weight and size of seed determine the amount of food-material immediately available for the plantlet, at the time of germination, it is to be inferred that these factors might have some influence upon production. Early experiments by Hellriegel, Wollny, Marek, and others were favorable to the view that seed of greater size and weight give generally more vigorous plants than those smaller or lighter. Much additional experimental work has been reported in recent years, and some of this evidence should be considered with respect to a few crops.

The problem is not so simple as it seems. Viewing the matter from the standpoint of the factors readily recognized, the effect of the accumulated food-materials is certainly to start the seedling off vigorously. If the cotyledons of the bean or pea are removed even during the late stages of germination, the plants thus deprived of a portion of their resources fall behind in growth. It is to be expected that the final effect of this loss would depend much upon the conditions subsequently encountered. If the season is bad, or the soil poor, the seedling with more potentiality in itself should be able to become established more safely and quickly, and the advantage secured might persist. Hellriegel supports the view that differ-

ences at maturity between the product of heavy and light seed are intensified when the conditions are unfavorable. With all conditions favorable, differences at first evident might, in time, disappear. In all cases, comparisons are only fair within the variety.

Hicks and Dabney have made a test of the relative effects of weight upon vigor, using many sorts of seeds. They attempted to eliminate all unsound seed, consequently the material was sieved and afterwards hand selected. The results are as follows: —

Experiments with Heavy and Light Seeds

Name and Variety	Number of Seeds in Each Lot	Weight of Seeds[1]	Number Germinated	Number of Plants weighed in Each Lot	Number of Days of Experiment	Weight of Seedlings
		Grams				*Grams*
Radish, early long scarlet	100	*A* 1.770 *B* 1.037	*A* 73 *B* 84	58	24	*A* 49.5 *B* 31.5
Vetch, winter	50	*A* 4.077 *B* 2.099	*A* 48 *B* 47	47	15	*A* 33.0 *B* 18.0
Sweet pea, Her Majesty	50	*A* 6.092 *C* 4.045	*A* 46 *C* 47	41	26	*A* 58.0 *C* 44.4
Cane, Early Amber	100	*A* 2.411 *B* 1.360	*A* 43 *B* 48	43	40	*A* 23.5 *B* 12.0
Kafir Corn, red	100	*A* 3.298 *B* 1.741	*A* 90 *B* 49	47	39	*A* 22.0 *B* 13.0
Rye, University of Minnesota, No. 2	50	*A* 1.105 *B* .745	*A* 45 *B* 45	45	23	*A* 34.5 *B* 20.0
Oats, White Wonder	50	*A* 1.298 *B* .805	*A* 50 *B* 49	49	23	*A* 37.2 *B* 25.0

[1] *A*, heavy; *B*, lighter than *A*; *C*, lighter than *B*.

From these results it seems just to conclude that, in general, a more vigorous growth, and consequently a better stand in the field, is secured by employing only the heavier seed.

235. Experiments with wheat. — The effect of size of seed on production has been with no other plant so extensively studied as with wheat. The evidence is most contradictory. The majority of the results seem to favor the view that large or heavy seed are preferable, especially when among the small seed are included distinctly immature grains. With wheat the factors are complex, for size may be considerably affected by plumpness, and the latter may be due largely to starch and water content. Additional starch in the grain may not affect the vigor and yield of the plant secured from such seed. Again, in the same variety, there may be different types or strains, — some with larger grains, some with smaller, although the yields may run practically the same. All these factors may affect the experiments. The results of grading and testing seed wheat are shown in subsequent tables.

In the first case reported by Zavitz, the seed were selected from both winter and spring wheats, and the experiments were continued five and eight years, respectively, but each crop was grown from previously unselected seed: —

Kind of Seed	Yield per Acre in Bushels	
	Spring Wheat	Winter Wheat
Large, plump	21.7	42.4
Small, plump	18.0	34.8
Shrunken	16.7	33.7

In the second case, reported by Hickman, to be contrasted with the preceding, "three grades were used: first grade, the large grains; second grade, the best of the grains passing through the sieve in screening out the first grade; third, unscreened wheat as it came from the thresher." The experiments were continued nine years, and after the first year, the selections for each were made from the same grade of the previous year: —

Yield for 9 Years, Bu. per Acre			Average Weight per Bushel		
First Grade	Second Grade	Third Grade	First Grade	Second Grade	Third Grade
15.48	16.06	16.03	57.8	58.3	58.1
17.16	17.64	16.69	52.2	57.9	58.1
16.11	15.82	16.06	57.7	58.0	57.4
16.25	16.50	16.26	57.6	58.1	57.9

There is also difference of experience with respect to large and small grains from the same head or plant.

236. Experiments with cotton. — Comparative production tests of the value of heavy cotton seed over the usual farm product have been made at the United States Department of Agriculture.[1] The heavy seed were separated, in the case of those varieties the seed of which are covered with fuzz, by special devices and methods. The field tests were made with results as shown in the table on the next page.

[1] Webber, H. J., and Boykin, E. B., "The Advantages of Planting Heavy Cotton Seed." U. S. Dept. Agl., Farmers' Bul. 285: 16 pp., 6 *figs.*, 1907.

Variety, Hawkins, Test at Lamar, S.C.	Yield in Pounds on Equal Areas, Each approximately One Acre			
	First Picking	Second Picking	Third Picking	Total Yield
Heavy seed (20 rows)	375	253¼	419	1047¼
Unseparated seed (20 rows)	335	228	381¼	944¼
Variety, Jones's Improved, Test at Hartsville, S.C.				
Heavy seed (14 rows)	158¾	793	212⅞	1164⅝
Unseparated seed (14 rows)	139	715¾	221⅛	1075⅞

In these two cases, the gain from the use of heavy seed is respectively 10.9 and 8.25 per cent. This is by no means a trifling gain when reckoned as additional profit per acre.

237. Experiments with tobacco. — Among practically all varieties of tobacco there is great difference in the size

Fig. 108. Tobacco plants from seeds of different sizes; heavy, medium, and light seeds respectively employed, from right to left. [Photograph from Bureau of Plant Industry.]

and weight of the seed from similar individuals. Trabut[1] found it possible to effect a separation into heavy and light sorts through the capacity of these two kinds, respectively, to sink or float in water. It was found that the heavy seed produced plants which were greener, more vigorous, and of larger size. Shamel has made further studies of this relation, separating, by means of a current of air, the seeds into three categories — heavy, medium, and light. Samples of these seed were germinated, and the accompanying illustration shows the relative vigor of the plants resulting from the different grades.

LABORATORY OR SUPPLEMENTARY WORK

Write a report upon the vitality of seed as affected by methods of harvesting and storage, consulting the literature accompanying this chapter, also such of that contained in recent volumes of the Experiment Station Record as may be readily available.

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CHAPTER XVI

THE TEMPERATURE RELATION

A LARGE number of species of plants composing the main vegetation of the earth are seldom, if ever, exposed within their normal ranges to great extremes of temperature. There are many annuals which first appear after the dangers of severe frosts are past, and they perfect their fruits long before the growing season is closed. A considerable number of perennials may be exposed to extremes only in a resting or semidormant condition. In general, then, native plants have been long acted upon by the particular climatic factors of the region, so that they show in a telling manner the influence of a long line of ancestry whose development and survival within the region is at least relatively fixed.

238. Climatic extremes and introduced plants. — Introduced plants in any region are, generally speaking, much more likely to suffer exposure to an injurious extreme, especially cold; yet exceptional conditions may bring disaster to any type of vegetation. The peach in the South and Southwest is sometimes in blossom before the winter is at an end, and the blossoms are not infrequently caught by late frosts. The famous peach belt of Michigan was visited in 1905 by an early frost in October, and the result was the practical annihilation of the peach

industry in that section, for the wood of the peach trees was entirely "unripened."

Throughout a large portion of the zone of its culture the cotton plant on well-watered and rich land grows continuously until killed by frosts. In the same way the nasturtium and the tomato may be in full growth when killed by frost. To a less extent this is true for familiar native plants of the field. In spite of these facts, the impression should not prevail that the vegetative period of a plant is so fixed by heredity and ancestral adjustment as to be incapable of responding fairly rapidly to the new environment. In a new region the growing season of a species or variety may be changed noticeably within a very few years. Corn from the far South with a growing period of six months will, if at all able to maintain itself in the North, modify its period of growth so that it will mature well within the season. Relatively few crops, however, are able to survive and propagate themselves if left to form fruit and germinate in the open, and in the relation of cultivated crops to temperature the question is more complex than is generally assumed.

239. Temperature and production. — As one goes northward in the United States or in Europe, a certain general change of crops is evident, indicating the universal importance of the temperature factor in modifying production. Potatoes may be grown from Mexico to Maine, but throughout this whole range the growing season is well within the normal length of the Maine summer. In fact, in the far South two crops may be grown during a single season. Corn is produced in the same region, but certain strains of field corn grown in the South might not reach

maturity unless protected during the first season in New England. The cotton and the cowpea disappear entirely in a little more than half the range of corn, while timothy and barley, almost unknown southward, approach their prime near the northern limit of this area.

In any scheme of continental plant zones, temperature is recognized as most important. In general, such zones are, therefore, constructed with special reference to the annual or seasonal isotherms. No scheme of regions based largely upon a single factor is entirely satisfactory. It is better, however, than no attempt at classification. Koeppen, Schimper, and others have indicated, on a broad basis, the plant zones of the earth, and Merriam has arranged for North America a suggestive scheme of life and crop zones (Fig. 2).

240. Cardinal temperatures. — Certain cardinal temperatures are recognized. "Maximum" and "minimum" are terms referring respectively to the highest and lowest temperatures at which the development of a particular organism may occur. It is apparent, however, that there may be separate maxima and minima for every process or activity of the plant. The maximum temperature for germination may be below that which will support continued growth in the developing plant. It is difficult, or at least inconvenient, to determine the most favorable temperature for any process or function; yet, within certain limits, such determinations are possible. The most favorable temperature is designated the optimum. It is also customary to employ the terms "ultra-maximum" and "ultra-minimum," denoting respectively the death point at high and at low temperature. The following tables from

Haberlandt give a comparative view of the relation of some familiar plants to these cardinal temperatures: —

CARDINAL TEMPERATURES FOR GROWTH, DEGREES C

	MINIMUM	OPTIMUM	MAXIMUM
Buckwheat	0–4.8	25–31	37–44
Hemp	0–4.8	37–44	44–50
Oats	0–4.8	25–31	31–37
Rye	0–4.8	25–31	31–37
Rape	0–4.8		
Wheat	0–4.8	25–31	31–37
Barley	0–4.8	25–31	31–37
Flax	0–4.8		
Pea	0–4.8	25–31	31–37
Sunflower	4.8–10.5	31–37	37–44
Maize	4.8–10.5	37–44	44–50
Pumpkin	10.5–15.6	37–44	44–50
Tobacco	10.5–15.6		
Melon	15.6–18.5	31–37	44–50
Cucumber	15.6–18.5	31–37	44–50

CARDINAL TEMPERATURES FOR GERMINATION, DEGREES C.

PLANT	MINIMUM	OPTIMUM	MAXIMUM
Zea Mays	9.4	34.0	46.2
Phaseolus multiflorus	9.4	34.0	46.2
Cucurbito Pepo	14.0	34.0	46.2
Triticum vulgare	5.0	29.0	42.5
Hordeum	5.0	29.0	37.5

These figures should be considered as merely suggestive, for it is apparent that differences in varieties, in local ad-

justment, and also in environmental factors will affect the cardinal temperatures in any particular case.

Reference has been made already to the fact that photosynthesis, metabolism, and other processes or responses of the plant are to a certain point rapidly accentuated with increase of temperature. Blackman has shown very clearly that maximum activity, especially for respiration and photosynthesis, has commonly been placed too high, since proper consideration of the time factor has not always been given.

241. Inhibition at high temperatures. — From recent work reported by Balls it would seem that the inhibition of growth at high temperatures during a considerable period of time is in all probability the result of an accumulation in the cells of injurious metabolic products. The time factor is most important. According to his views, some of these deleterious products are produced at low temperatures, but under such circumstances they are constantly decomposed, whereas at high temperatures production is more rapid, and consequently accumulation and injury result. Upon this hypothesis the effect of high temperature upon the protoplasm would be that of favoring auto-intoxication.

242. Heat units. — Considerable attention has been bestowed upon computations of the heat units (thermal constants) required to mature certain crops. Such data are not without interest, yet examination of the evidence thus far accumulated indicates that there is practically no such thing as a relatively invariable thermal constant for any plant when factors other than temperature are inconstant or uncontrolled. Assuming that every other factor of the

environment is constant, there is a theoretical thermal constant, and it is of sufficient importance to receive some practical consideration.[1]

243. Heat units and germination. — If the number of heat units required in order to bring a plant to maturity were at all constant, then the number requisite for any phase of growth should likewise be more or less constant. Some interesting data are available respecting germination, and in the following table the time intervals are given for germination at the temperatures indicated, and the heat units may be readily computed : —

Sinapis alba		*Linum usitatissimum*		Melon (Cantaloupe)		*Trifolium repens*		*Zea Mays*	
Temp. ° C.	Time	Temp. ° C.	Time	Temp. ° C.	Time	Temp. ° C.	Time	Temp. ° C.	Time
0.0	408	1.8	816	16.9	222	5.7	240	9.2	240–288
1.9	384			19.4	68	9.2	144	12.9	120–168
		4.8	408	25.05	44	12.9	72	16.9	90
5.7	96	5.7	144	28.0	74.4	13.0	69	21.1	42
9.2	84			40.6	94	17.05	62.4	25.05	23–44
12.9	41	12.9	66			21.1	42	28.0	36–48
17.2	41					25.05	42		
21.1	22	17.05	72			28.0	72		
25.05	36	21.1	36			34.0	192		
28.0	72–78	25.05	38						
		28.0	60–72						
		34.0	192						

[1] There are several methods of computing heat units. In each case it is necessary to know the period of growth in days and the daily mean temperature during the growing period. With this data we may then obtain the total heat units by multiplying the growth period by the daily mean temperature. This method makes 0° C. or 32° F. the basis. In the

Sum of Daily Mean Temperatures above 18° C. (64.4° F.) for Fruiting Period of Date-palm from May 1 to Oct. 31

Locality	Sum of Daily Mean Temp. above 18° C. (64.4° F.)		Remarks	
	Degrees C.	Degrees F.	Meteorological	Ripening
Algiers, Algeria	652	1,174		No dates ripen.
Orleansville, Algeria	788	1,418		Very early sorts mature.
Fresno, Cal.	1,054	1,897		Sorts grown usually fail to ripen.
Tucson, Ariz.	1,409	2,538	Obs. 6 yrs.	Sorts now grown usually fail to ripen.
Cairo, Egypt	1,593	2,868		Dates ripen regularly.
Phœnix, Ariz. (Salt River Valley)	1,677	3,019		Many sorts ripen regularly.
Biskra, Algeria	1,836	3,304		Date culture the leading industry. Even Deglet Noor ripen.
Ayata, Algeria (Oued Rirh region)	1,906	3,431	Temp. 1891	Deglet Noor dates ripen, but not always well.
Tougourt, Algeria	2,049	3,689		Do.
Bagdad, Mesopotamia	2,356	4,242		Many excellent varieties ripen.
Indio, Cal. (Salton Basin)	2,237	4,027	Obs. 7 yrs.	
Salton, Cal.	2,679	4,823	Obs. 12 yrs.	

case of the F. scale it is necessary, of course, to subtract 32 from the daily mean before multiplying for the product. It would seem, however, that the method of computation to be preferred is one whereby an approximate growth minimum is taken as the basis, and the difference between this and the daily mean represents the daily efficiency during the growing period. An example in the latter case is as follows: assuming the growth period of wheat to be 100 days, the minimum growth temperature 40° F., and the daily mean to be 70° F., we have $70 - 40 \times 100 = 3000°$ F.

244. The date-palm. — One of the most important applications of a study of the relation of plants to the heat units of the region in which they are grown is that made by Swingle respecting the date-palm. He has shown that as the heat units increase, the general adaptability of arid regions to date culture is advanced, and a certain minimum may not be exceeded for any type of date. From such a study it was considered possible to foretell with approximate accuracy what section of the Southwest might be utilized in date culture.

245. Control of temperature. — It is obvious that limitations of expense impose pronounced restrictions upon the exercise of control over the temperature factor in the open. With a few intensive crops, such as asparagus, waste steam has been utilized to some extent in forcing in open culture, but proper control of temperature for forcing or for producing crops out of season is usually confined to greenhouse and hot-bed culture.

In some sections of the United States the loss of the entire peach, apple, or other fruit crop may occur in consequence of one or two late frosts, when, as experience has shown, the temperature may fall from 4 to 14° below freezing.[1] Recently a control or prevention of this loss has been successfully accomplished by means of coal or oil heaters. The general plan is to place from 60 to 100 small ovens or heaters per acre at appropriate distances apart. Then, if by midnight the indications are that a freezing temperature will be reached in the early hours of

[1] Paddock, W., and Whipple, O. B., "Fruit-Growing in Arid Regions." (Frost Injuries, Secondary Bloom, and Frost Protection.) Chapter 19: 324–354, 1910.

morning, usually the coldest period of the day, the heaters are lighted. It has been found possible at an average cost of about $20 per acre to raise the temperature of the orchard as much as from 5 to 14° F. above that of the normal air, and this often in the face of considerable wind. The practice has recently assumed unexpected importance, and seems to have superseded the relatively ineffective smudge methods.

246. The temperature of the plant. — The temperature of the plant is in general the temperature of the environment. Twigs, branches, and even trunks of trees will show during cold weather changes of temperature more or less in accordance with that of the air. In the case of large branches or trunks some time will be required in order that the minimum of the air may be registered by the tree, and there will be, therefore, a very definite temperature lag.

In the sunshine dark buds, branches, or trunks may absorb heat to such an extent that the internal temperature will be greater than the external. In the same way, green leaves exposed to sunlight show a temperature from two or three to fifteen degrees higher than the air, depending upon the intensity of the light. This latter point has received careful attention by Blackman, who has employed in the work very delicate electro-thermometric methods. The ordinary method of wrapping the bulb of a thermometer with one or more thicknesses of a leaf will not afford accurate indications of the actual leaf temperature.

247. Adjustment of structure. — There are few or no protective structures in plants which are of direct service against injurious temperatures. As will be shown later, both high and low temperatures act upon the plant cell to

cause drying out, and the structures which are ordinarily assumed to be protective against cold or heat are in reality serviceable in preventing loss of water. The delicate young buds of the peach or other deciduous trees may be inclosed by bud-scales, hairs, and resins; nevertheless, such buds promptly freeze solid when the temperature falls below the freezing-point of the cell-sap, or the point of supercooling. The trunk of the tree is, of course, protected in a way by thick bark, yet so far as the entrance of cold or loss of heat is concerned this protection is insignificant.

248. Irritable response. — Through growth movements toward or away from a source of heat, plants commonly exhibit the capacity for irritable response (positive and negative thermotropism) with respect to temperature; but this response is of little practical significance, except as further evidence of the paratonic relations of the organism. Thermonastic movements also occur, but this general class of phenomena is discussed in section 306.

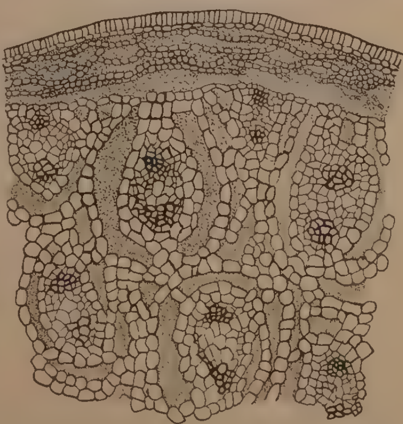

FIG. 109. Frozen stem of Fritillaria, showing ice-masses (stippled). [After Müller-Thurgau.]

249. Freezing. — Some of the results of freezing deserve careful consideration. It is well known that

in the freezing of a plant cell under ordinary conditions, the ice crystals are formed upon the surfaces of the cells. In the case of tissues with intercellular spaces these crystals form in the latter. In this way the protoplasm gives up its water and the mechanical injuries of the ice crystal are not ordinarily exhibited within the protoplast. In the case of very rapid supercooling of large cells it is probable that ice crystals develop within the cell; thus mechanical harm may result. Similarly, in tissues mechanical injury may sometimes result, and the bark of immature wood may be ruptured when severely frozen. It has been found, however, that the diameter of a frozen twig is usually less than normal.

In view of all the facts which have been presented by various investigators, it would appear that the ability of a plant to withstand cold is in large part determined by the capacity of the cells to give up water without injury during freezing. On the other hand, according to the views of Molisch, death from cold commonly results during the process of freezing. This refers particularly to active cells, or herbaceous shoots, and is at variance with the popular impression that frozen plants are less injured when thawed out gradually.

Fig. 110. Frozen leaf-stalk of Lavatera, showing ice-masses (black). [After Müller-Thurgau.]

Many plants are injured at temperatures above the freezing-point. This may be due to a simple disturbance of the water relation, but it is more probable that there

are complex effects, the permeability of the protoplasm being also affected.

250. Buds. — The relation of buds to cold has received careful attention by Wiegand. He finds that ice may form in a large number of species when the temperature falls as low

FIG. 111. Section of a bud of *Populus nigra* frozen at 5° F. sectioned and photographed in the open; light areas are ice crystals. [After Wiegand.]

as − 18° C. At this temperature it may be formed in large quantities and is more abundant in cortical and parenchymatous tissues than in meristem. When absent at this temperature, it may be assumed that the tissue is made up of very small cells with thick walls and low water-content. This is explained by the fact that " the degree of cold necessary to cause the separation of ice is proportional to the

force which holds water in the tissue. This, in turn, depends upon the relative proportion of water to cell-wall and protoplasm." Measurements were made by Wiegand of seven species of trees frozen at a temperature of $-18°$ C. and of seven species which failed to freeze. The comparative data for two species in each group are presented by the following table: —

	Cell Diam. in mm.		Texture of Wall	Per Cent of Water
	Max. Aver.	Min. Aver.		
A. Ice abundant in leaves and growing points at $-18°$ C.				
Cratægus punctata	0.040	0.012	thin	49.4
Prunus serotina	0.021	0.015	thin	47.6
B. Ice not present at $-18°$ C.				
Quercus alba	0.015	0.006	thick	22.7
Carya alba	0.048	0.015	very thick	31.4

LABORATORY WORK

Effect of heat and cold upon germination. — Expose selected dry seed of barley or peas for 1 hour to dry-oven temperatures of 50° C., 75° C., and 100° C. Place 25 of each lot in a germinator together with an equal number of control seed and determine the effect upon the percentage of germination. In the same way employ seeds of the above plants in water at the temperatures above given, and test similarly. For further comparison it is also desirable to employ in both experiments a lot of seed which are just beginning to germinate. Discuss the results.

Soak some seed of barley or peas an hour or two in water and keep another lot dry. Expose lots of 25, soaked and unsoaked, to such low temperatures as may be conveniently prepared by freezing mixtures of salt and ice. One lot may be placed in test-tubes immersed in broken ice, another in similar tubes at from 5 to 10° below zero, and another exposed to about − 20° C.; from − 5 to − 10° C. may be obtained in a freez-

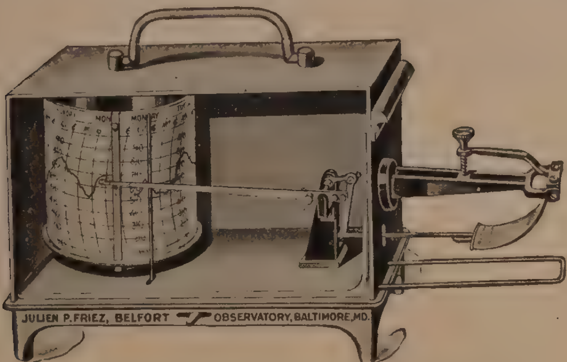

FIG. 112. Thermograph. [Illustration from Julien P. Friez.]

ing mixture of 10 parts common salt to 100 parts snow, while − 20° C. requires 33 parts salt. Subsequently, test the germination and discuss the results.

Formation of ice crystals. — Place filaments of Spirogyra in a drop of olive oil in a hanging-drop culture. Expose in a chamber surrounded by a freezing mixture such that the temperature of the chamber is reduced to about − 10° C., then remove the culture and examine promptly under the microscope to locate position of any ice crystals formed.

On a day when the temperature of the air is about 0° C., or below, make sections of artificially or naturally frozen buds and locate the ice crystals.

Effects upon root elongation. — By means of the method employed in the study of growth, mark with parallel lines on the

root-tips of germinating beans, and study the effect upon elongation of such different temperatures as may be obtained in the incubators at hand, in the refrigerator, and at the room temperature. In all cases the beans employed should be uniform, and the experiment should be carried out in a moist atmosphere.

Temperature relations. — In case time has not permitted, in the appropriate place in connection with various phenomena discussed, to experiment upon the effects of changes of temperature, such experiments should be included here, as far as possible; especially important are the effects of temperature upon transpiration, photosynthesis, enzyme action, and growth.

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CHAPTER XVII

THE LIGHT RELATION

ALL green plants exhibit direct relations to intensities of light. The influence of light in the synthesis of the first organic products, or photosynthates, has been considered; and it is now necessary merely to indicate some of the more general ecological relations.

251. The adjustment of plant members. — No phenomenon of plant life is more familiar than the turning of leafy shoots toward light or the orientation of leaves in a manner to occupy a favorable exposure. Plants placed at the window of a dark room promptly show the effects of the light stimulus. The same relations may be observed in the field. The capacity to show through growth curvatures an irritable response to light from one side is called phototropism. We have to distinguish as main classes of responding structures those axes which are parallelotropic, curving in such manner that the tips point toward or away from the source of light, and those which are plagiotropic, or at some angle. Leaves are transversely phototropic, and the response secures a favorable illumination of the chlorophyll bodies. As a result broad-leaved plants develop commonly to form a more or less perfect mosaic, no better examples of which can be found than those of the grape-vine or Boston ivy. The adjust-

ment of the single shoot, of the plant as a whole, or of a group of plants is of the same nature, ample consideration being given to other forces which may be operative at the same time. Trees thickly branched, such as the Norway maple and the linden, or the unpruned apple and pear, will exhibit in a significant manner this effect, exposing a complete shell of leaves. (See Chapter XX for growth movements.)

When trees grow up close together in the forest the lower branches are ultimately too much shaded, so that these are killed and in time drop off. The leafy shoots are confined to the uppermost parts, and this system of constant self-pruning through the survival of those favorably placed results in the characteristic long trunks of the forest trees as compared with the shorter trunks and abundant branches of isolated specimens in the lawn or meadow. The tall trunks are, of course, most desirable from the standpoint of the lumberman; but, at the same time, the decayed branches or stumps offer favorable opportunity for the entrance of destructive fungi which cause great annual loss through the decay of sap or heart wood, and thus artificial pruning possesses great advantages.

252. Light perception. — Phototropic organs may possess special perception regions, and these regions do not necessarily correspond to those of curvature or bending. The method of perception is not understood, but the sensitiveness of the mechanism is almost incredible.

The perceptive mechanism resulting in leaf orientation has received much attention. Haberlandt and others find in the lens-shaped cells and cuticular thickenings of epidermal cells the structures which they regard as indirectly

important. In these cells the light may be focused in some basal region of the protoplasm, and through the unequal illumination the stimulus to orientation is supposed to be given. It has been demonstrated photographically that these cells focus the rays, but since such cells occur under a variety of conditions, and for many other reasons, they are not positively connected with this form of irritability.

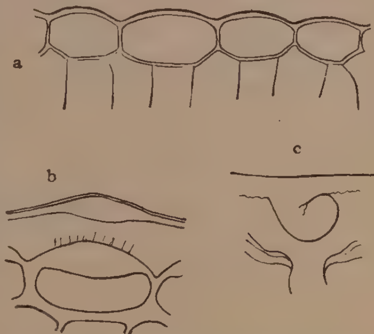

Fig. 113. Epidermal modifications which focus light rays; Berberis (*a*), Rhododendron (*b*), and *Prunus Lauro-cerasus* (*c*). [After Haberlandt.]

Important in the orientation is the direct or indirect sensitiveness of the petiole. Wager believes "that the perception of light is bound up with its absorption by the chlorophyll grains, in which case the palisade cells would be the percipient cells."

253. Diverse requirements. — From casual observation of plant habitats, it may be noted that there is great diversity in the light intensity under which different species grow to maturity. Many plants reach perfection only when exposed, but others develop more vigorously under the partial shade of the forest or thicket. Exposed and shaded situations usually differ with respect to other environmental factors, such as humidity and evaporation; and in a careful study of habitats it is necessary to measure and to attempt an evaluation of all factors.

It has been reported that during a unit interval the evening primrose utilizes in direct sunlight about three times as much CO_2 as when in diffuse light, while the common polypody works more effectively in the latter. Many shade-loving plants may reach maturity in light which is reduced to about $\frac{1}{50}$ the intensity of maximum sunlight. Beyond a certain light intensity the plant gains little, for the small amount of CO_2 in the air is then the limiting factor in growth. Temperature is a further limiting condition. In the warm forest of the tropics there may be a vigorous forest-floor vegetation, but the cold shade of a far northern forest affords only a scant undergrowth.

254. Light intensity. — Upon the surface of the earth light intensity varies considerably both diurnally and seasonally, depending, of course, with a clear sky, upon the altitude of the sun. The possible daily maximum is at sun-noon, June 22. If this intensity should be represented at the equator by 100, then with a growing season in the north temperate zone approximately from March 21 to September 23, or its equivalent in the southern hemisphere, the light intensity from 9 A.M. to 3 P.M. would be represented approximately by 82 to 98 and the noon variation by 93 to 98, as calculated by Clements for Lincoln, Neb. From this it is apparent that the variation in light intensity throughout agricultural regions with a clear sky during the growing season is not considerable. Range of intensity in the open is in general insufficient seriously to affect vigorous growth, although it may modify form and chemical content. In some regions cloudiness may be an important factor.

255. Injurious effects. — It has long been well estab-

lished that injury may result from continuous or lengthy exposure to intense light. Many of the simpler green algæ may be killed by an exposure to brilliant sunlight of less

FIG. 114. Effect of light upon a plate culture of *Pseudomonas campestris;* colonies have appeared only where the plate was protected by a letter (W) screen. [After Russell and Harding.]

than one hour. It has been shown conclusively that strong light inhibits the action of various enzymes. The diastases are notably affected, so that the conversion of starch in a

clear solution may be readily prevented by exposure to light. The chlorophyll of shoots protects in a measure the diastase from the injurious action of light during the day. Nevertheless, from this and other causes starch conversion in the leaf is reduced to a minimum during days of bright sunshine.

Bacteria and other hyaline microscopic organisms are killed by direct sunlight, and this fact is important in sanitation. The convincing demonstration of the effect of sunlight upon bacteria was made by Ward. He prepared cultures of the bacteria upon clear agar in Petri dishes, and then exposed the dishes to sunlight. It was determined that the organism causing anthrax, *Bacillus anthracis*, may be killed in such cultures in direct sunlight by an exposure of from a few minutes to several hours, depending upon the intensity of the light. Striking results were obtained by covering the dish to be exposed with a black paper or metal stencil so that the contrast between exposed and unexposed parts of the plate may be sharp. A spectrum was also thrown upon prepared cultures and it was determined that the blue-violet rays constitute the effective killing portion of the spectrum. With the use of glass covers or globes the injurious rays are to a considerable extent excluded.

256. Artificial light. — Interesting studies have been made upon the use of artificial light in greenhouse culture, as in forcing lettuce, endive, radish, and certain flowers. In such experiments the artificial light has been employed usually at night, or supplementary to daylight. Economically, artificial light is probably a failure, owing to the expensiveness of it; but the results of the experimental work bring out some points of interest.

By the use of the protected electric arc during half of the night Bailey was able to hasten lettuce two weeks. The

Fig. 115. Lettuce of the same age under normal sunlight (above) and with electric arc a part of the night in addition (below). [After Bailey.]

naked electric arc yields light distinctly injurious to the majority of crops. This injury is due to the richness in ultraviolet rays, which, as already shown, are destructive to protoplasm. When screened by glass, clear or opales-

cent, the harmful rays are largely excluded. Continuous night illumination with the electric arc may promote more rapid growth in some plants, but with others there is a tendency to run to seed.

The incandescent electric light, which is relatively rich in red rays, has been successfully employed by Rane in forcing lettuce. By the use of the acetylene light Craig has found it possible to force the growth of radish, lettuce, and a few other crops; but the best results were with flowers, Easter lilies especially giving increased production in a shorter time.

FIG. 116. Field peas grown for equal periods in white (*a*), blue (*b*), and orange-yellow (*c*), light.

257. Monochromatic light. — Many experiments have been made to determine approximately the effects of light of different wave lengths on the form and structure of plants. In much of the work which has been done pure screens were not employed, yet his type of work is sufficiently important to justify careful physical methods. In general, the dry weight of plants grown for a considerable period under monochromatic

screens is greatest in red, and least in violet; yet the growth in red is not equal to that in white light. The violet rays are also important in the production of bloom.

In the following table there are given, after Teodoresco, the relative areas of leaves developed from the bud in different qualities of light during a period of about thirty days. With each plant the leaves occupied equivalent positions on the young shoot:—

EFFECT OF WAVE LENGTH UPON AREA OF LEAVES, AREAS IN SQ. MM.

PLANT EMPLOYED	KIND OF LIGHT				
	White	Red	Green	Blue	Darkness
Vicia Faba	948.3		127.8	654.8	52.8
Lupinus albus	158	49.5	38	62	8
Polygonum Fagopyrum (cotyledons)	128	59	23	64	11
Ricinus sanguineus (cotyledons)	1105	503	200	600	53

The next table indicates the thickness of the leaf under the different conditions of illumination, and also the number of stomata on equal areas of the lower surface:—

PLANT EMPLOYED	WHITE		RED		GREEN		BLUE	
	Th. Leaf μ	No. Stom.	Th. Leaf μ	No. Stom.	Th. Leaf μ	No. Stom.	Th. Leaf μ	No. Stom.
Vicia Faba . . .	671	4	337	7	297	12	332	7
Arachis hypogæa .	243	12	216	18	207	20	216	13
Ricinus sanguineus	346	2	256	6	218	10	297	6
Lupinus albus . .	352	14	210	31	195	38	271	25

258. Half-shade in plant propagation. — In conservatory and greenhouse production of certain tropical plants whose habitats are naturally the moist, shady woods, some form of shading has commonly been practiced. It is only in this manner that many delicate ferns and succulent species are grown successfully. The same purpose is effected by the cloth-covered tents or slat-covered sheds

FIG. 117. A coffee plantation in a Hawaiian forest. [After Van Leenhoff.]

often employed in southern climates, ostensibly to diminish the light, but also to insure higher humidity and to protect against wind and frost. As a result of such work it has become apparent that partial shade may be advantageous in many horticultural or even farm crop operations. The demand for vegetable products out of season is an ad-

ditional incentive to the use of any device which may regulate or control the conditions of the environment.

259. Crops responding to half-shade. — In general half-shade increases succulence and delicacy, so that it is particularly applicable to such crops as asparagus, cauliflower, celery, lettuce, and radish. It is employed in forcing rhubarb, in the cultivation of ginseng, and has proved especially important in pineapple culture in Florida. Sumatra tobacco, grown for wrapper purposes in the Connecticut valley and in other regions, has been greatly improved by half-shade conditions. Half-shade is also necessary in many cases to the maintenance of proper conditions for seed beds, and it is essential in the nursery propagation

Fig. 118. Peas grown 6 days in darkness (*a*), in about ½ light (*b*), and open in greenhouse (*c*).

of many forest trees. A thorough study of the relations of seedling trees to half-shade operations is greatly to be desired in the advancement of forestry work generally.

Many bush fruits and other agricultural products are commonly grown in the partial shade of other plants. It is generally believed that currants are benefited by the partial shade of grapes or certain tree-fruits, provided the water-content of the soil is not seriously affected. Coffee and tea are more profitably produced in subtropical regions in forest glades, or when partially shielded by occasional trees. In southern Algeria and other portions of the Sahara shading is practiced on a large scale in the oasis cultures. The protecting palms improve the conditions for figs, peaches, and other fruits, under which, in turn, vegetables may be grown, provided only that the water-supply is adequate. On the other hand, the production of grapes, with higher sugar content for wine purposes may require a selection of slope insuring best exposure to light during a certain period of growth and maturity. Fruit trees are grown on the southern sides of walls in England and France, and it would appear that both the additional light and heat thus obtained are advantageous.

In many parts of the United States, especially in the Central West, lettuce and other salad crops become bitter and undesirable for table use with the stronger light and heat of the summer season. The shade tent, properly employed, will permit the constant summer culture of such crops. The strong flavor of radishes produced during the summer are also modified and improved by partial shade.

260. Morphogenic effects. — The comparative effects

of light and darkness upon the form and growth of plants has been much investigated. In most cases no adequate

FIG. 119. Sun print showing difference in opacity (thickness and chlorophyll content) of celery leaves grown in half-shade (left) and in sunlight (right).

consideration has been given to other factors than light, but in general the response to light is so much more marked

than to other factors that the errors are perhaps negligible. When the buds of ordinary herbaceous plants with central axes are permitted to develop in the dark there is a marked elongation of the internodes and a suppression of branches. Shoots from tubers or tuberous roots affording constant food-supply will show this characteristic in a striking manner. The leaves of such herbaceous plants are usually

Fig. 120. Sumatra tobacco under cloth tent, Connecticut Valley. [After Shamel.]

greatly reduced in size, and sometimes restricted to mere scalelike structures. On the other hand, when the light intensity is reduced to from 20 to 40 per cent of normal sunlight, the leaves may be increased to twice their size in direct sunlight, as demonstrated by many experiments upon lettuce, tobacco, and other broad-leaved plants. When produced in the dark, the radicle leaves of such plants as the rhubarb develop in a short time petioles of unusual extent and delicacy, while the leaf blade remains small.

This effect is of much practical value in the forcing of rhubarb for early market (Fig. 87).

The leaves of tobacco produced in the shade tent are not only larger, but thinner, and they possess relatively larger air spaces and more spongy parenchyma; the fibrovascular bundles, or venation systems, are less prominent, and the leaf is thereby improved for wrapper purposes. In the fibrovascular bundles of half-shade plants the mechanical supporting tissues are usually reduced, and this is a factor in blanched celery. Self-shading to produce crispness and tenderness may be practiced in some cases; thus in the cultivation of Cose lettuce, romaine, and cauliflower, the simple operation of bringing together and tying the leaves in the form of a head may produce the effect desired.

261. Half-shade and quality. — Plants grown in half-shade commonly contain a higher per cent of moisture and less ash. It has been ascertained that the apparent acidity of strawberries is increased by shade. This apparent increase is, however, due to lessened accumulation of sugar in the berries.

The aromatic products of plants are not important as animal nutrients, but they are physiologically essential, and represent almost the sole value of many economic plants used as condiments. In 1838, De Candolle called attention to the diminished production of savors and odors in shaded plants. It was found later that plants removed from southern latitudes to the latitude of Scandinavia during the two months of maximum sunshine in the latter region, showed an increase in the development of aromatic products. Indeed, it has long been suggested that many

fruit-bearing plants containing objectionable flavors might be improved by reduced light.[1]

262. The effect of shading upon other environmental

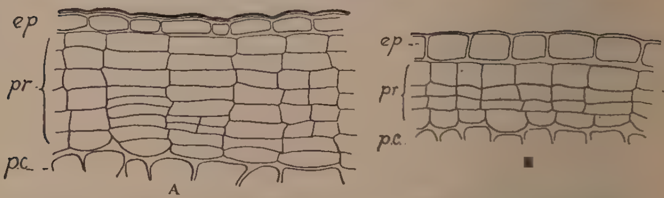

FIG. 121. Bark of *Acer Pseudo-platanus*; epidermis (ep), periderm (pr), primary cortex (pc); developed in white light (A) and in red light (B). [After Teodoresco.]

factors. — From the preceding statements it has been noted that half-shade may modify in a direct manner other conditions of the environment. The factors commonly affected are the following: (1) moisture conditions of the soil; (2) rate of evaporation; (3) humidity; (4) temperature; (5) air movement; and (6) certain biological relations. The tables on the next page indicate the effect of the usual shade tent (made of unbleached cotton) upon soil moisture and evaporation (first table after Whitney).

Much remains to be determined respecting the modifications in plants induced by shading, and likewise extensive studies are required to evaluate the different factors involved. From the indications already presented, it is

[1] Schuebeler, Bonnier, and Flahault have shown that in northern climates flowers are more highly colored and plants commonly richer in essential oils. It is also well known that plants rich in volatile oils and other aromatic products are numerous in the Mediterranean region, a region in which the rainy season is confined largely to the winter months, and the summer is practically a continuous exposure to intense sunlight.

obvious that many of the effects conveniently discussed under "shading," in the sense of "half-shade," are in large part the results of changes in the water or moisture relations. The relation of shade plants to fungous diseases also deserves a more careful study.

Table of Soil Moisture Inside and Outside of Shade (Cloth) Tent

Date	0–3 Ins.		0–9 Ins.	
	Inside	Outside	Inside	Outside
July 1	15.2	12.3	15.6	13.6
July 2	15.0	13.3	15.4	14.0
July 3	15.2	13.4	15.3	14.3
July 4	13.7	11.5	14.9	13.4
July 5	12.8	9.9	13.5	12.1
July 6	12.1	9.7	13.9	11.8
July 7	12.0	8.4	14.0	10.8
July 8	12.2	7.8	13.1	10.5
July 9	11.5	6.9	13.0	9.8
July 10	11.0	6.3	12.7	8.7

Evaporimeter Readings, Shade-tent Experiments, Ithaca, N.Y., 1908

Date	Cc. of Water Lost by Standardized Evaporimeters		
	Closed Tent	Tent Open North	Exposed
Aug. 11–23	96	163	263
Aug. 23 — Sept. 1	85	162	240
Sept. 1–8	80	140	210
Sept. 8–15	75	110	170

LABORATORY WORK

Orientation. — Make and record observations in the open or in the greenhouse upon the relations of shoots and leaves of any plant to light. Begonia, grape, or Norway maple may be used; also note the relations of the compass plant (*Lactuca Scariola*) if available.

Place a pot or water culture containing seedlings (several centimeters high) in a chamber permitting one-sided illumination. The chamber may consist of a tight box, black on the inside, arranged with a slit on one side through which rays of light may be admitted. Place the plants as far as possible from the source of light, and for some hours note the response of the shoot (and also of the root if a water culture is employed). Expose another plant which has been in complete darkness to one-sided illumination for some moments and then return it to a dark chamber. Note any subsequent response and discuss the results.

Light perception. — Make hand sections of leaves of oats, hyacinth, hepatica, *Saxifraga Geum*, or *Garrya elliptica*, and describe the lens-shaped cells or epidermal modifications considered by Haberlandt and some others to be light-perceptive organs. Consult the article cited by Wager, note his method of photographing objects through cells, and read his conclusions regarding light perception.

Wave length and rate of growth. — With bottles, test-tubes, and corks prepare three pieces of apparatus as shown in Fig. 122. Prepare the solutions of (1) ammoniacal copper carbonate and (2) naphthol yellow, so as to give practically pure colored lights (spectroscopically tested, if possible), the one excluding practically all except blue and blue violet rays, and the other excluding all except the red end of the spectrum. Fill one bottle three fourths full with each of these solutions and one with water. Place in each test-tube, on filter paper or moss, a germinated seed of the field pea, and insert the tubes as shown in the figure. Relative growth may be observed until the seed have outgrown the chambers. With the apparatus commonly

at hand, it is impracticable to attempt to compute equal energy intensities of the colored lights.

Light intensity. — Determine the relative value of light in the open and contrast it with the light intensity in the greenhouse and in the shade of vegetation or buildings. To make this study use the ordinary photographic actinometer, the device employed by Clements,[1] or strips of solio paper. If the latter are employed, it is simplest to determine the length of exposure in seconds necessary to bring the paper to a certain standard shade of brown. This may be done by previously following the changes in the paper while contrasting it with a brown color scheme, choosing some shade of color in the color scheme as a standard which is invariably one of those attained by the paper in the process of darkening.

Etiolation. — Place in a perfectly dark chamber water cultures of peas, potatoes, and onions sprouting on moist moss, and any potted plants available. Make accurate observations of the conditions of the plants or buds when placed in the dark, and, if possible, arrange control cultures exposed to the light, but under similar conditions of moisture and temperature. After ten days or more, make comparative observations, noting the effect (1) upon structures

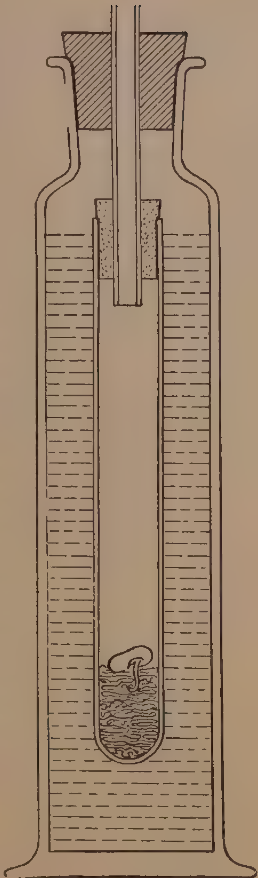

FIG. 122. Simple apparatus for qualitative tests of the effects of light of different wave length.

[1] Physiology and Ecology, pp. 72–75.

developed in the dark; (2) upon structures formed previous to placing the plants in the dark.

Secure the same variety of any plant grown in half-shade and in an exposed situation; compare the two with respect to structural modifications, water-content, and extent of root system.

FIG. 123. Potato sprouting in a dark, moist atmosphere.

Light and blossoms. — Place over carnations, just coming into blossom, aërated bell glasses, one of the bell glasses being covered with manila paper or unbleached cotton. Follow the effect of severe shading upon the opening of flower-buds of other plants which were equally advanced at the outset.

Killing effect of light. — Prepare in a Petri dish a dilution culture of any species of bacteria convenient, using the minimum quantity of the clearest agar obtainable. When the agar is solidified, expose the cultures about one hour to direct sunlight, protecting, however, a portion of the dish by means of darkened cardboard. Replace the cover of the dish, incubate the cultures for several days, and note the effect of the exposure to light. This experiment cannot be carried out where laboratories are not equipped for the cultivation of micro-organisms.

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CHAPTER XVIII

RELATION TO DELETERIOUS CHEMICAL AGENTS

A LARGE number of water-soluble chemical substances are injurious to all living protoplasm at concentrations considerably below the osmotic equivalent of the cell-sap. Such injurious substances are poisons, or toxic agents. These may act directly or indirectly upon the protoplasm, and the inference is that the action is ultimately chemical. The dilution of a deleterious agent often results in stimulation, whilst at still further dilution this effect also disappears.

There is at present very incomplete knowledge of toxic action; yet many advances have been made within the past quarter-century. These advances have served to increase knowledge generally, and in agricultural lines they have been important in the study of soils, bacteriology, plant pathology, and entomology. The results have been utilized in the interpretation of experiments with fertilizers, in improving methods of disinfection or purification of water-supplies, in the protection of plants against insect pests and fungous diseases, and in various other ways to which subsequently subsidiary reference may be made.

263. General relations to poisons. — Toxic agents may be general or specific poisons. Specific poisons are as yet

of minor importance in plant work. General poisons are usually either strong (such as salts of mercury), or weak (alcohol) for all organisms. Nevertheless, plants may show some specific adjustment to poisons, and diversity in effect may be due to one of the following causes: —

(1) A certain selective absorption may be shown, as in the case of the nutrients, so that penetration will be rapid in one case and practically prevented in another.

(2) Upon penetration the deleterious substance may be converted into a relatively insoluble and nontoxic form, before effecting serious injury to the protoplasmic organization.

(3) There may be specific differences in the effects upon protoplasm, — peculiarities which it is at present impossible to explain definitely.

One parasitic fungus may be killed by a dilute solution of a copper compound, and another may germinate in a relatively concentrated fungicide. Again, alkaloidal or other toxic organic bodies may be produced within living tissues, where they seem to set up no particular disturbance; whereas they may serve as strong toxic agents when placed in contact with other cells or organisms. In the fermentation of fruit sugar the common yeast plant produces alcohol, which soon prevents the growth of other micro-organisms. Brown has demonstrated a marked selective permeability in the coverings of seeds of a variety of barley. These seeds take up water from a fairly strong solution of sulphuric acid, and remain uninjured; but mercuric bichlorid penetrates them with comparative ease.

264. Comparative resistance. — The fungi and bacteria are commonly much more resistant to toxic agents than are

species of seed-plants; that is to say, many fungi and bacteria may grow in solutions which would inhibit root growth. However, aërial surfaces of seed-plants do not, as a rule, permit the rapid absorption of water or of chemical agents, so that for crop protection such surfaces may be covered with strengths of toxic solutions prohibitive to the germination and growth of fungi, as in the use of fungicides and insecticides.

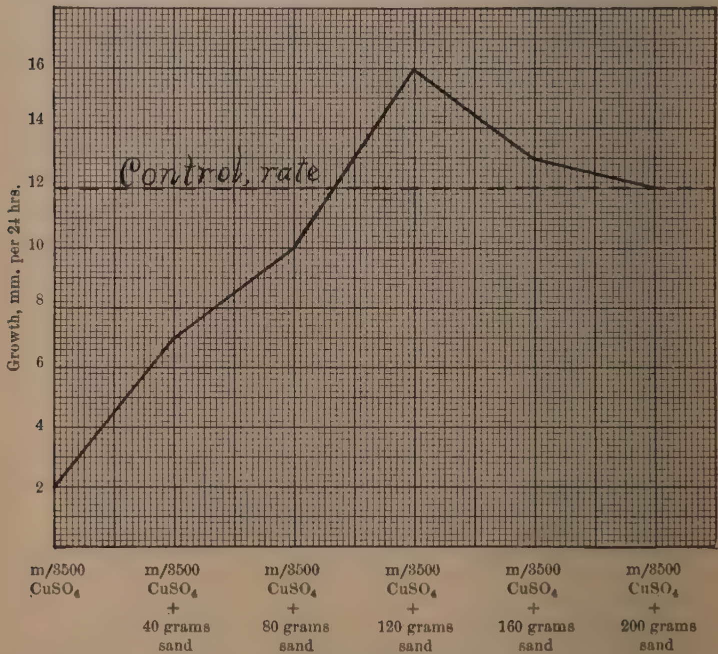

FIG. 124. Depression of toxicity with addition of sand. [After True and Oglevee.]

FIG. 125. The toxic action of $Al_2(SO_4)_3$ in different substrata, all containing a nutrient solution except no. 6: n/40 (1); n/70 (2); nutrient solution (4); n/20 (5); control, distilled water (6).

Many species of the lower algæ are particularly sensitive to certain toxic agents, such as the salts of copper and other heavy metals. Zoöspores of fungi and some species of bacteria pathogenic in animals may be equally sensitive.

265. Toxic action and the substratum. — Much of the literature of toxic action is confusing, owing to the fact that the results are not comparable. Substances usually exhibit their greatest toxicity in distilled water. Any nearly neutral nutrient solution reduces toxic action even in cases where molecular readjustments would not seem to be important. In the soil complex physical and chemical conditions prevail, and these further modify toxic action.

Solid particles, such as pure sand, graphite, and filter paper, may reduce toxic action to a considerable extent. True and Oglevee found that twice as much sand as solution may reduce the toxic action of $CuSO_4$ for *Lupinus albus* as much as thirty-two times (Fig. 124). The method of reducing toxicity by solid particles is usually denoted adsorption. It is a phenomenon explained upon the hypothesis that many molecules or ions of the toxic substance are physically held by the surfaces of the particles of the inert material, and are, for the time, removed from the possibility of chemical action. Another explanation is that the solid substances offer obstacles to the free movement of the solvent particles. Possibly both views are important. Many of the so-called absorptive properties of soils both respecting fertilizers and deleterious agents are in reality adsorptive.[1]

[1] The table from Jensen, on the opposite page, affords a comparison of toxic action in sand and in solution cultures.

From the data presented, it is evident that in defining toxic concentrations it is necessary to speak in terms of the substratum. When soil cultures are employed, the type of soil and amount of organic matter are important. The nutrient solution may modify the action of a poison by forming with it chemical combinations less diffusible or dissociated, and ultimately less injurious. Again, there may be antitoxic action, as in the calcium-magnesium relation. Mass action is also important, as suggested by Dandeno; thus a seedling injured by 5 cc. of a toxic agent may be killed by a greater quantity of the same concentration.

266. Method of action. — It is not possible at present to state definitely the method of action of all deleterious agents. Many metallic salts and other substances precipitate protein, and it is easy to picture the immediate disturbance of protoplasmic organization effected by such

Toxic Agent	Soil Culture (Quartz Flour with Nutrients)		Solution Culture (with Nutrients)	
	Parts of an N/10,000,000 Solution			
	Inhibiting Growth	Stimulating Growth	Inhibiting Growth	Stimulating Growth
$Ni(NO_3)_2$	70,000– 60,000	5,000– 1,000	5,000– 2,500	4–2
$ZnSO_4$ . .	300,000– 100,000	3,000– 1,000	7,000– 6,000	none
$AgNO_3$.	300,000– 100,000	90,000– 10,000	1,000– 900	20–10
$CuSO_4$ . .	300,000– 100,000	10,000– 4,000	10,000– 5,000	none
Fe_2Cl_6 . .	600,000– 400,000	90,000– 20,000	100,000– 8,0000	4,000– 2,000
$Pb(NO_3)_2$	500,000– 300,000	90,000– 40,000	400,000– 200,000	20,000–10,000
Phenol .	200,000– 100,000	8,000– 4,000	200,000– 100,000	8,000– 4,000
Alcohol .	7,500,000–2,500,000	750,000–250,000	7,500,000–2,500,000	75,000–25,000

agents, yet it is impracticable to adopt a special grouping based upon a similarity of action within the cell. Among the deleterious agents known, those of economic significance are of special interest. Of these the important groups are inorganic and organic acids; caustic alkalies; salts of the heavy metals; formalin; alcohol and anæsthetics;

FIG. 126. Indications of the effects of the substratum upon the toxic action of $CuSO_4$; loam (L), sand (S), graphite (G). [Photograph by W. W. Bonns.]

various organic compounds, including decomposition and hydration products of proteins and lecithins, alkaloids and miscellaneous nitrogenous bodies, also many non-nitrogenous organic products of diverse composition; and certain deleterious gases of the carbon series.

267. Inorganic and organic acids. — Inorganic acids are usually the most toxic of the acid substances for the higher

plants. Some of the results secured by Kahlenberg and True are given in the table below, where also a comparison may be made with acetic acid, the latter occupying an intermediate position with respect to toxicity among organic acids:—

Acids	Pisum sativum		Zea Mays		Lupinus albus	
	Gram Mol. Sol.	Parts Per Million[1]	Gram Mol. Sol.	Parts Per Million	Gram Mol. Sol.	Parts per Million
HCL . . .	1/12800	3	1/3200	11	1/6400	5.5
H_2SO_4 . . .	1/12800	3	1/3200	11	1/6400	5.5
HNO_3 . . .	1/12800	3	1/3200	11	1/6400	5.5
CH_3COOH .	1/3200	11	1/400	91	1/1600	22.5

In these experiments the roots of a few seedlings were immersed in 300 cc. of solution (the acid in distilled water) and the concentrations given are just sufficient to kill at least 50 per cent of the roots after an exposure of 24 hours. The toxicity of inorganic acids is strikingly reduced by the presence in the solution of solid particles.

268. Alkalies. — Alkalies are in general less toxic to the roots of seed plants than are equivalent concentrations of acids or of salts of the heavy metals. In order to inhibit root growth of seedlings in water cultures, it requires from 5 to 10 times as strong a solution of caustic alkali as of a mineral acid. Alkalinity (basicity) and acidity as applied to field conditions are merely relative terms, since under such conditions the usual methods of determining these qualities are inaccurate. It is well known, however, as in-

[1] Approximate.

FIG. 127. The toxic action of aluminium salts, and control cultures:— Distilled water (1, 3); nutrient solution, strong, denoted X — $\frac{1}{5}$ X, and $\frac{1}{25}$ X (5, 6, 7); $Al_2(SO_4)_3$ n/200, n/1000, and n/5000 (17, 18, 19); $Al_2(SO_4)_3$, as preceding, with nutrient X (8, 9, 10); $Al_2(SO_4)_3$, as preceding, with nutrient $\frac{1}{5}$ X (11, 12, 13); $(Al_2SO_4)_3$ with nutrient $\frac{1}{25}$ X (14, 15, 16); Al_2Cl_6 series (20–25) corresponding to six of the preceding (8–13).

FIG. 128. The toxic action of aluminium salts; this series corresponds exactly to that in Fig. 127 except that here the cotyledons were removed.

dicated under the discussion of lime, that many plants thrive under basic conditions, while others yield best when the substratum is acid.

269. Salts of the heavy metals. — The salts of the heavy metals constitute a group of the most toxic agents known. The various soluble inorganic salts of the same metal are commonly of about equal toxic value. The table given below is comparable to that given for inorganic acids, the concentrations representing those which kill the majority of the roots in 24 hours: —

Substances	Pisum sativum	Zea Mays	Lupinus albus
	Gram Molecular Solution		
$CuCl_2$	1/51200	1/102400	1/25600
$CuSO_4$	1/51200	1/102400	1/25600
$NiSO_4$	1/51200	1/51200	1/25600
$Ni(NO_3)_2$	1/51200	1/51200	1/25600
$CoSO_4$	1/25600	1/6400	1/12800
$Co(NO_3)_2$	1/25600	1/6400	1/12800
$AgNO_3$	1/204800	1/204800	1/204800
Ag_2SO_4	1/204800	1/204800	1/204800
$HgCl_2$	1/204800	1/51200	1/12800
KCN	1/12800	1/6400	1/6400

Kanda employed pots holding two liters of soils in some experiments with horse beans. These were in one case watered daily with copper sulfate to such extent that at the end of three weeks the pot contained 26.394 grams of the salt. This amount caused only a slight reduction of root growth, but stem growth was greater than in the control.

Copper compounds are extremely injurious to certain

algæ. They have been effectively employed by Moore and Kellerman [1] for the eradication of such organisms in ponds and water supplies. For this purpose copper sulfate is used at the rate of 1 part to 250,000–1,000,000 parts of water. A copper coin in a small dish of water containing half a dozen threads of a green alga is sufficient to cause death in a day or two.

270. Formalin. — Formalin is a penetrating toxic agent for all plant cells. According to Clark it ranks close to mercuric bichlorid and silver nitrate as a poison for fungi in beet decoction. In agricultural practice formalin solutions are important in the control of certain fungous diseases by seed treatment. The seed do not absorb the solution so rapidly as the spores, so that a short immersion may serve to disinfect the former. Formalin is employed for the prevention of bunt of wheat, loose smut of oats, and potato scab.

271. Organic bodies. — The effects of various alkaloids and other nitrogenous bodies upon the higher vertebrates have long been a matter of experimentation. The toxic products of disease-producing bacteria are of this nature. Such substances are frequently more toxic to organisms possessing complex nervous and circulatory systems; but similar substances may be injurious to protoplasm in general. Through the decomposition of animal or vegetable matter in the soil, toxic bodies may be formed, and these may at times play a recognizable rôle in the relations of vegetation.

272. Root excretions. — De Candolle made the suggestion more than half a century ago that plants may influence

[1] Bureau Plant Ind., U. S. Dept. Agl., Bul. 64 : 44 pp., 1904.

one another by means of substances derived from their roots. This view was at first credited, but soon lost support. Rotation of crops is based largely upon the idea of physical advantage, or disease suppression. In very recent years some investigators have proposed that soils are commonly unproductive on account of the presence in them of toxic organic compounds. This view with some persons implies that the injurious substances arise through the excretions of roots. The assumption of any general excretion of toxic bodies by roots is at present scarcely justified, although an oxidizing power of roots is now demonstrated.

273. Unproductiveness. — Interesting and valuable data have been accumulated by Schreiner and his associates, which throw much light upon the nature of the organic compounds which may be found in the soil, and likewise upon their toxicity. The decomposition of root-hairs and cast-off portions of roots, of green manures, or of any plant or animal remains in the soil give rise to temporary products which may be injurious. Nevertheless, it is not believed that the quantities of injurious organic bodies set free in a well cultivated soil during the growth of a staple crop, whether due to the decomposition of roots or to direct excretion, are often sufficient to be of agricultural importance. With the large number of bacteria ordinarily present in the soil, and the amount of aëration necessarily given in cultivation, such toxic substances would seem to be of merely temporary concern. In the case of bog soils, or land where there is insufficient drainage and lack of aëration, the toxic factor may be permanently important. It is certain that unproductiveness is not due to a single factor of this type, and at present many lines of work are

being directed toward a solution of the problems of infertility.

274. Relative toxicity of some organic compounds. — In the table below are given some of the interesting results obtained by Schreiner and Reed respecting the effects of various organic compounds upon wheat placed in water cultures from 7 to 10 days; the concentrations indicated are in parts per million (p.p.m.) in distilled water : —

Substances	Lowest Conc. causing Death, p.p.m.	Lowest Conc. causing Injury, p.p.m.	
Alanine		500	Only roots injured at 500.
Tyrosine		10	
Leucine			No injurious action.
Choline		500	Roots most affected.
Neurine	250	25	
Betaine			No injury.
Guanine			No injury.
Guanidine . . .	100	1	
Skatol	200	50	Roots more injured.
Pyridine		50	

Among twenty-two nitrogen-containing compounds, two were found which were injurious at the surprisingly low concentration of less than 10 p.p.m. In the above experiments water cultures were employed; but tests by Bonns in my laboratory have shown that wheat in paraffined pots containing rich garden loam is practically unaffected by pyridine at the enormous rate of 8000 p.p.m., this solution being used to moisten the soil to 60 per cent of its water-holding capacity. If this relationship should

be found to hold good for the other organic substances mentioned, it is apparent that the accumulation of such bodies in the soil in amounts which might be toxic (wholly neglecting the possibility of their immediate destruction) would require long periods of irrational cropping.

275. Illuminating gas. — It has long been known that illuminating gas is injurious to vegetation. Even small leaks in gas pipes are fatal to the roots of trees in the vicinity. Vegetation in cities suffers greatly from this cause. The danger is greatly increased by the fact that gas diffuses through the soil to considerable distances, particularly when the surface of the ground is frozen or compact, as when streets or roadways supervene. Many decorative plants are reported to fail as house plants when illuminating gas is burned. This may be due to gas-escape at the time of lighting burners (since, as will be shown subsequently, the amount of gas needed to cause injury is extremely small), or it may be due to incomplete combustion of the gas.

Crocker and Knight have shown that ethylene, although present in very minute quantities, is apparently the chief toxic constituent of the illuminating gas with which they worked. They employed as indicators flowers and buds of the Carnation, — Boston Market and the pink Lawson. After an exposure of three days the young buds of these plants were dead, and bursting buds were prevented from opening by a concentration of one part of gas in 40,000 parts of air; while after an exposure of twelve hours 1 part to 80,000 caused the flowers that were already opened to close. In ethylene of 1 part in 1,000,000 buds in which the petals were just showing failed to open after an ex-

posure of three days, and flowers closed after an exposure of twelve hours to an atmosphere of only 1 part to 2,000,000.

276. Stimulation by means of weak toxic agents. — Small quantities of acids and other substances may serve as stimulants in several types of enzyme action, — they may increase the velocities of the chemical reactions. The transformation of starch by diastase and of certain proteins by pepsin are both accelerated by traces of acid. Richards and Ono have shown conclusively that the dry weight of certain fungi in nutrient solutions may be increased two or three times by the addition of a small quantity of one of several metallic salts.[1] In general, zinc has afforded the best results. Spore production is diminished in the stimulated cultures. Furthermore, it has been shown by subsequent work that stimulated plants are able "to dispose more economically of the sugar used, . . . thereby permitting a more rapid production of dry substance in a given time."

[1] The data from some experiments (Richards) in which the fungus was grown on a nutrient solution containing sugar are as follows: —

STIMULATION OF GROWTH IN ASPERGILLUS NIGER BY $ZnSO_4$
(CULTURES KEPT AT 30° C. UNLESS OTHERWISE NOTED.)

SPECIAL CONDITIONS OF CULTURE	PERIOD OF GROWTH, DAYS	WEIGHT IN MILLIGRAMS					
		No $ZnSO_4$	.002 % $ZnSO_4$	.004 % $ZnSO_4$	.008 % $ZnSO_4$	.016 % $ZnSO_4$	.033 % $ZnSO_4$
	7	335	730	760	765	770	715
	6	300	670	700	680	650	610
Asparagin added .	6	560	970	980	770	390	250
Peptone added .	8	1120	1490	1375	1515	1455	1280
2 % $FeSO_4$ added .	6	650	630	680	650	645	610
24° C.	6	200	335	350			

The results of stimulation experiments in which seed-plants have been employed are somewhat contradictory. On the whole, a certain degree of stimulation seems possible, especially when some of the conditions of growth are unfavorable. From investigations conducted in Japan

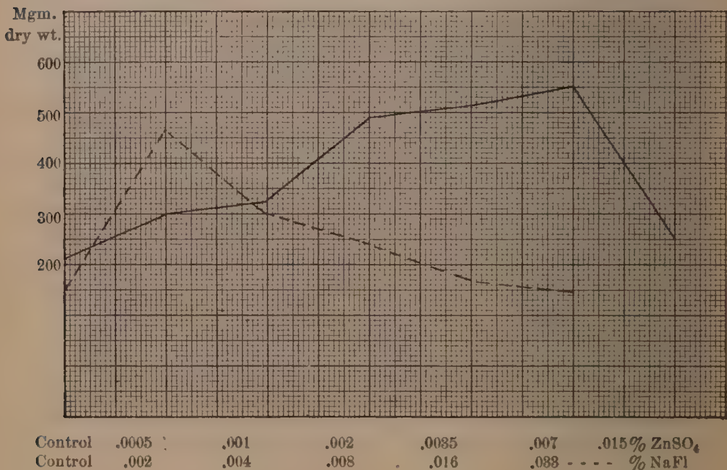

FIG. 129. Stimulation of growth in Aspergillus by $ZnSO_4$ (continuous line) and NaFl (broken line). [Data from Richards.]

there have been reported some benefits from the joint action of iron and manganese, also with salts of iodin, sodium fluorid, and some other agents, yet some of the effects are probably indirect.

277. Protection of crops by insecticides and fungicides. — Practically all cultivated or exploited crops are subject to the attacks of insects and fungi. More than twenty-five important species of insects are known to at-

tack the grape-vine and there are at least half as many fungous diseases of the same plant. Numerous instances might be cited in which the number of fungous and insect pests of a particular crop is as great as those indicated.[1] On the other hand, there are cultivated crops which require very little consideration with respect to parasites of any kind.

It is only in relatively recent times that spraying operations have developed, especially spraying to prevent fungous diseases. This type of control has been in large part due to a careful investigation of the relations between plants and toxic solutions on the one hand, and to the development of effective spraying devices on the other. In nearly all cases protection against fungous diseases and insect pests is effected by covering the surfaces of fruit, leaves, and stems with a poisonous substance, which should, while relatively noninjurious to the host, prevent the effective germination and penetration of the spores, or kill the insects concerned.

In controlling insects, it is to be remembered that there are two great classes with respect to the method of attack; these are: —

(1) Chewing insects which bite off and eat the vegetative parts of the plant; for example, cabbage worms, tent caterpillars, and potato beetles, which would be killed by poisons sprayed upon the plant.

(2) Sucking insects, or those which get their food by in-

[1] Some estimates of the amount of damage annually sustained by the crops of the United States have been made, and taking as a basis the prices at which the crops actually sell, it seems to be demonstrated that the vast sum of one billion dollars may be aggregated.

serting a beak directly into the tissues, for example, plant lice and squash bugs.[1]

278. Destruction of weeds by poisons. — For years it has been more or less customary to employ salt for the destruction of weeds in the lawn or garden, or to suppress all plants growing in walks and playgrounds. It is only within recent years, however, that any special study has been bestowed upon the use of toxic solutions in the form of sprays as one of the recognized methods of weed control in lawns and cultivated fields. It is not a method which may be expected to replace the usual practices of clean cultivation, rotation, or pasturing, nor is it one which should lead the grower away from a close study of the rooting and reproductive habits of weeds.

[1] The poisons or insecticides commonly employed for biting insects are such as Paris green, arsenate of lead, arsenite of soda, arsenite of lime, London purple, and hellebore. Of these, Paris green is by far the most important. The use of this substance attracted general attention between 1860 and 1870, when the Colorado potato beetle became an important factor in potato production. Shortly afterwards, the same mixture was employed throughout the South against the so-called army-worm of cotton, and it has since been used to give protection against an endless number of biting insects.

In employing the usual means of control against sucking insects, such substances as kerosene emulsion, miscible oils, whale oil soap, and lime-sulphur wash may be used, as well as methods of fumigation. The first three substances mentioned may be employed, with care, upon the foliage and growing parts. Miscible oils, carbolic acid, and relatively strong kerosene may be used only when the plant is in a dormant condition. Fumigation with tobacco smoke is common. The highly toxic vapor of hydrocyanic acid, prepared from potassium cyanide and sulfuric acid, has also been employed in the fumigation of trees under tents and with nursery stock in a dormant condition. It may also be used in the greenhouse with care, but special instructions are needed in any particular case.

The effective use of chemical agents as protective measures against fungous diseases, dates from the discovery of Bordeaux mixture by Millardet in France, 1883. Since that time, there has been organized throughout the United States and in foreign countries extensive methods of controlling these diseases.

279. Deleterious substances employed. — Common salt is only slightly toxic, yet it has been much employed on

FIG. 130. Greater ragweed in untreated field of wheat. [Photograph by H. L. Bolley.]

account of its osmotic action. It may be used dry in roadways and other situations, and it has sometimes been effective in suppressing broad-leaved, delicate weeds in

lawns, where it may be applied at the rate of from 3 to 6 pounds per square rod. Crude carbolic acid possesses an

Fig. 131. Wheat in plat contiguous to that in Fig. 130, showing effect of iron sulfate spray on ragweed. [Photograph by H. L. Bolley.]

objectionable odor, but it is very effective in killing vegetation in walks or courts. It may be sprayed upon the ground at a strength of 1 quart of the acid to 5 gallons

of water. Waste formalin at the rate of 1 pound to 10 gallons of water may be used under similar circumstances.

Copper sulfate and iron sulfate are, however, the two compounds which may be commercially employed with hand or power sprayers for the suppression of certain weeds in fields of grain or flax, and in large lawns. Copper

FIG. 132. Wild mustard of size effectively reached and readily injured by the spray.

sulfate is commonly used as a solution containing from 3 to 5 per cent of the salt, — 12 to 20 pounds to 50 gallons of water. It is usually recommended to employ iron sulfate at a strength of $1\frac{1}{2}$ to 2 pounds of the salt per gallon of water.

280. Practicability of the chemical method. — The chemical method may be wisely employed under certain circumstances, as follows: —

(1) Upon ground where no vegetation is desired — walks, playgrounds, courtyards, etc.

Fig. 133. Natural growth of dandelions in an untreated lawn. [Photograph by H. L. Bolley.]

(2) When particularly undesirable weeds are present in small spots, and the temporary suppression of all growth is not a serious objection.

(3) When it is desired to suppress weeds or to prevent weed seeding during the maturity of a seed crop.

Fig. 134. Lawn with dandelions, similar to that in Fig. 133, but treated with iron sulfate two weeks before blossoming. [Photograph by H. L. Bolley.]

(4) When, during the growing season of the crop, a majority of the undesirable weeds are more sensitive than the crop grown.

It is obvious that the use of chemical sprays for weed eradication in the field is dependent upon the resistance of the crop as compared with the weed and to the penetration of the chemicals employed. This method has been found especially applicable in growing cereal crops, grasses, flax, and peas.[1]

The plants which are killed are those whose surfaces are easily wet by the spray, but there are some plants, the common plantain (*Plantago major*), for example, which, although wet, is almost unaffected. Those which are not wet generally possess smooth glaucous leaves, or are provided with a waxy bloom. In any plant the succulent or rapidly growing portions are more easily killed. Thus it follows that this means of eradication may be generally employed for plants with an indefinite habit of growth.

LABORATORY WORK

Toxic action. — Determine the limiting concentrations of $CuSO_4$ and H_2SO_4 for inhibition and growth of roots of corn and peas. Use the tumbler-culture methods employed in the study of mineral nutrients, or, if observations cover only a short interval of time, the germinating seeds may be pinned to the lower surfaces of corks covering the vessels employed, the roots projecting into the solutions. Make decinormal stock solutions of the toxic agents. With the $CuSO_4$ employ at least

[1] From a considerable number of experiments, it has been found that such plants as the following are more or less readily killed: bindweed, Canada thistle, dock, great ragweed, lamb's quarters, mustard or charlock, orange hawkweed, sow thistle, wild buckwheat, and wild radish. Weeds which have not been successfully combated without injury to the growing crop are such as bentgrass, bull-thistle, couch-grass, horse-tail, pigweed, and others. With iron sulfate Bolley has been able to hold the dandelion in check ; but on account of the perennial root, this plant is one of the most difficult to eradicate.

four or five dilutions between $\frac{N}{10000}$ and $\frac{N}{300000}$; while with H_2SO_4 prepare dilutions ranging from $\frac{N}{800}$ to $\frac{N}{8000}$.

Effect of insoluble particles. — After following carefully the discussion in the text, determine, through cultures in tumblers, the concentration of $CuSO_4$ and of H_2SO_2 which will inhibit and permit growth in (1) granulated quartz or infertile sand, and in (2) a rich garden loam. In these experiments use, in each case, sufficient of the solution to moisten the substratum approximately, and in comparative experiments the same amount of solution should be used. Permit the experiments to run only one week, and watering will not be required.

Toxic agents and foliage. — With a hand spray or atomizer treat the foliage of convenient plants in the greenhouse or field with 3 per cent copper sulfate, and 5 per cent iron sulfate. Study the comparative effects. Cereals, grasses, carnations, and onions may be taken as types of foliage not easily wetted, while dandelions, mustard, beans, and peaches will furnish suitable contrasts.

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CHAPTER XIX

VARIATION AND HEREDITY

In organic variation, our interest centers on the mechanism and forces concerned in the adjustment of an organism to its environment. Variation signifies change, and may be evidence of past and present influences; heredity gives a record of the past and certain promises for the future. Both of these are important aspects of evolution.

Many theories have been advanced in explanation of the facts of variation and heredity. No single theory receives at present universal sanction. Every reasonable hypothesis merits careful consideration, and the present widespread interest in experimental evolution makes it particularly desirable to view new facts in an unprejudiced light. The limited scope of this book makes it possible to include only a brief presentation of some of the important facts and views, as an introduction to the subject; the fuller theoretical treatment and application must be sought in the literature.

VARIATION

The capacity for variation is a fundamental possession. It is universal with living organisms. Though heredity

characteristics of parents are transmitted to the offspring, yet not all individual characteristics of all ancestors are transmitted. The offspring may exhibit modification. This modification may be evident under constant conditions, or it may occur in response to environmental changes. It may be an acquirement manifest merely during the life of the organism, or it may be innate and transmissible. Every organism possesses an individuality.

281. Individuals and species. — Individuals which resemble one another closely and which have a common origin may collectively constitute what may be called a race, variety, or species. Our ideas of such groups are based upon a study of individuals (few or many, small or large populations) and naturally center about average examples. We recognize, however, certain extremes; in fact, there are multitudinous variations, for there may be as many extremes as characters, or character combinations. These extremes, perhaps, have in many cases so insensibly entered into other recognized varieties that opinions would differ in determining to which variety a particular individual should be attached. Some varieties, on the other hand, may stand apart with sharply differentiated characters; within these, individuals may also differ perceptibly among themselves. In any case, a group of individuals, such as a race, variety, or species, is in a measure a theoretical average with respect to characters, and is made up of a series of individuals showing in the different characters considerable fluctuation.[1]

[1] All organisms resembling one another closely must look alike to the inexperienced eye, — to the eye unfamiliar with the group. Upon close inspection and measurement, however, relatively wide differences

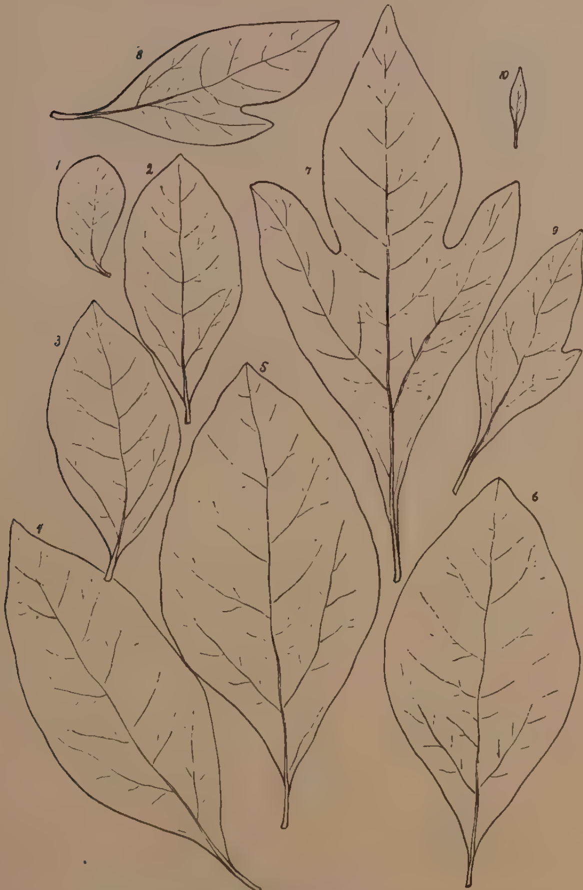

FIG. 135. Variation in the leaves from a single bud of sassafras.

282. Fluctuating variation. — The minor differences which all individuals of any population exhibit are commonly fluctuating, or continuous, variations. The ideal, or type, which these individuals approach is an average individual, with reference to a number of characters. If many individuals be examined with respect to any one character, the result may be given in the form of a curve of variation. An examination, for instance, of a population of the common field daisy would disclose a variation in the number of ray flowers; thus there might be from 10 to 20. This variation in number represents the range, and the numbers 10, 11, 12, 13, etc., constitute the variates or classes. Perhaps the majority of the population would have the same number of ray flowers, say 15, which class would then represent the mode, or class of greatest frequency. In a normal curve there would be a diminishing frequency towards both higher and lower classes. Quetelet has shown that this curve, in the main, corresponds with the law of probabilities, or curve of frequency of error.

invariably appear. The tomato is an excellent example of variability. Little more than a century ago it was introduced as a vegetable. To-day its varieties are numbered by the hundred, and there are a great many well-defined types and forms of fruit, characters of leaf, size, etc. We are thus sure that by one means or another variation has been effected, and in a marked degree. Once several strains or varieties are developed, hybridization is the greatest possible source of variation, or multiplication of forms.

The use of score cards in judging corn, apples, and other farm and horticultural crops draws special attention in a practical way to standards among economic plants, and at the same time to departure from the standards, — to variation. The producer is likely to have in mind as an ideal the best or most highly developed type of any variety or strain, and thus in the work of selection he may constantly depart from the old ideal in the direction of a new and improved strain.

The symmetrical curve shows the highest frequency, or mode, in the center, but not infrequently the mode is considerably shifted from one side to the other, giving skew curves. Again, multimodal curves occur, and many other subsidiary forms have been found to prevail in certain species or races.

283. Darwin's theory of natural selection. — Through his wide experience with living things Darwin was thoroughly conversant with the existence of fluctuations in nature. It was apparent that growers select, isolate, and breed desirable forms or individuals, excluding or destroying those undesirable. Such a process appears to have led to the origination of new breeds and races. Darwin saw in nature similar forces yielding similar results; viewing the problem, therefore, in the uncontrolled or natural environment, he formulated the following ideas: (1) any individual variation, slight or considerable, which enables the organism possessing it to succeed or maintain itself better than its neighbor will have a strong chance of becoming perpetuated; (2) more seeds are produced than can grow again unto seedage, more organisms enter upon life than can be reared; (3) those less well equipped for life's struggle succumb, and there is manifest a powerful process of Natural Selection.

He would seem to have maintained that the main line of evolutionary progress and change lies in the natural or artificial selection of relatively minute variations; that is, natural selection lays hold upon fluctuating variations. There is constant variation, hence there is constant change, or evolution. Wide variations arising suddenly, termed sports, or discontinuous variations, were apparently

regarded by Darwin as of less importance in evolutionary progress (see section 287).

In most of the present-day discussions respecting evolution, natural selection is recognized as a potent force; but great diversity of opinion prevails with regard to the magnitude of the variations by means of which progress in selection is maintained.

284. Rate of increase. — A study of the theoretical rate of increase of many organisms involves numbers which are not easily grasped. A single tobacco plant may produce from 500,000 to 1,000,000 seed. At the minimum production mentioned the second year there would be 250 billion seed, and the product the third year would be expressed by eighteen figures. At the rate of one seed per square foot, this number would plant the surface of the earth several hundred times over. A vigorous specimen of the common dandelion under observation produced in a season about thirty flower-heads, each averaging about 300 seed, or 9000 seed for the season. In this case, there would result at the end of the fourth season 6,561,000,000,000 seed.[1]

Assuming the capacity of an organism to vary, the power of the environment to suppress and exterminate unfitness makes it a very strong factor in determining the nature of

[1] One instance from the animal side may be cited (adapted from Jordan and Kellogg, "Evolution and Animal Life," p. 59), that of the quinnat salmon of the Columbia River. This is a prolific fish whose eggs and young are poorly protected and consequently devoured by numerous greedy enemies. A female will ascend the river when four years old and deposit about 4000 eggs, subsequently dying. Allowing for 50 per cent of males and the normal period of maturity of females, only five generations would be required, should all individuals survive, for this fish to occupy far more than the volume of the sea.

those creatures which survive. Since, moreover, the organisms which survive respond to the influence of the environment, be it much or little, the stamp of environment is ultimately borne by every living thing. This does not imply, however, that the environment stimulates change in the direction of fitness for the particular environment, yet a strictly physico-chemical explanation would perhaps demand this.

285. Fluctuating variation and the origin of varieties. — The artificial selection of fluctuating variations has been the basis of great improvement, or of the maintenance of standards, in many cultivated crops. The sugar content of good varieties of the beet has been increased from between 8 and 10 per cent to from 14 to 18 per cent. Many deny permanence to this type of selection, and much experimental work appears to be in progress, designed to throw light upon the question.

Punnett says: " The small fluctuating variations are not the materials on which selection works. Such fluctuations are often due to conditions of the environment, to nutrition, correlation of organs, and the like. There is no indisputable evidence that they can be worked up and fixed as a specific character." Castle, speaking of the heredity of fluctuations, says, " It is an exceedingly difficult and slow process, and its results of questionable permanency."

Physiological modifications in corn. — Unusually interesting experiments in corn variation and breeding have been conducted at the Illinois Experiment Station. In this case variation in chemical content with respect to high protein and low protein, also high oil and low oil, has been made the subject of study, and the results for a ten-year

period have been reported. A white dent corn was used, and to this the name Illinois has been given. In protein content the 100 ears of seed corn used the first year varied from 13.87 to 8.25 per cent. From the table in the note below [1] it will be seen that the ten years of selection sufficed to bring the *average* of the plat (1906) in high protein (14.26 %) above the best ear in the first crop (13.87 %), and the average in the low-protein plat (8.64 %) was practically as low as the lowest ear (8.25 %). The yearly averages in the high-oil and low-oil breeding show a variation often more striking than in the case just cited, as shown in the footnote.

[1] TEN GENERATIONS OF BREEDING CORN FOR INCREASE AND DECREASE OF PROTEIN

Year	High-protein Plot, Average Per Cent Protein		Low-protein Plot, Average Per Cent Protein		Difference between Crops, Per Cent
	In Seed planted	In Crop harvested	In Seed planted	In Crop harvested	
1896	——	10.92	——	10.92	.00
1897	12.54	11.10	8.96	10.55	.55
1898	12.49	11.05	9.06	10.55	.50
1899	13.06	11.46	8.45	9.86	1.60
1900	13.74	12.32	8.08	9.34	2.98
1901	14.78	14.12	7.58	10.04	4.08
1902	15.39	12.34	8.15	8.22	4.12
1903	14.30	13.04	6.93	8.62	4.42
1904	15.39	15.03	7.00	9.27	5.76
1905	16.77	14.72	7.09	8.57	6.15
1906	16.30	14.26	7.21	8.64	8.62

The relatively high protein content in the product harvested in 1901 is evidently the result of early maturity of the seed during that remarkably dry season.

Summarizing the extreme variations in these qualities at the beginning and close of the periods, the table on the next page is suggestive.

286. Pure lines. — Johannsen has employed the term "pure line" to denote the offspring of a single individual produced by self-fertilization (thus isolating a type, genotype). With pure lines he has conducted extensive selection experiments, and the results for quantitative characters stand in contrast to those obtained by selection in an ordinary population. Selection within a pure line, from modal individuals and from those showing the greatest deviation, yield offspring the averages of which are the same. According to this, selection within the

TEN GENERATIONS OF BREEDING CORN FOR INCREASE AND DECREASE OF OIL

Year	High-oil Plot, Average Per Cent Oil		Low-oil Plot, Average Per Cent Oil		Difference between Crops, Per Cent
	In Seed planted	In Crop harvested	In Seed planted	In Crop harvested	
1896	——	4.70	——	4.70	.00
1897	5.39	4.73	4.03	4.06	.67
1898	5.20	5.15	3.65	3.99	1.16
1899	6.15	5.64	3.47	3.82	1.82
1900	6.30	6.12	3.33	3.57	2.55
1901	6.77	6.09	2.93	3.43	2.66
1902	6.95	6.41	3.00	3.02	3.39
1903	6.73	6.50	2.62	2.97	3.53
1904	7.16	6.97	2.80	2.89	4.08
1905	7.88	7.29	2.67	2.58	4.71
1906	7.86	7.37	2.20	2.66	4.71

pure line cannot change the averages, or shift the mode. These results are most suggestive and important, and the principle has been confirmed by Jennings and others; but many additional data will be required before this type of behavior is recognized as of general significance.

TABLE SHOWING EXTENT OF VARIATION

TYPE OF BREEDING	BEST EAR	EXTREME VARIATION
High protein	per cent	per cent
1896	13.87	5.62 original seed
1906	17.67	10.94 tenth year selection
Low protein		
1896	8.25	
1906	6.73	
High oil		
1896	6.02	2.18 original seed
1906	8.51	6.91 tenth year selection
Low oil		
1896	3.84	
1906	1.60	

287. Mutations. — A sudden variation which is fully transmissible has been called by De Vries a mutation. It is a discontinuous variation or hereditary saltation. Mutation phenomena have become prominent in variation studies since the publication by De Vries of his Mutation Theory. Already the term has been loosely employed, but in general it has the special significance above indicated. De Vries advanced the view that all evolutionary progress is based upon the occurrence of mutations. His conclu-

FIG 136. Bud variation in Nephrolepis: fronds characteristic of five floricultural varieties on the same root system.

sions were primarily the result of extensive studies upon the evening primrose (*Œnothera Lamarckiana*), and upon a general review of available information respecting both the origin of domesticated varieties, and the behavior of organisms in nature. Even though some hesitate to accept all the conclusions arrived at for the Œnothera mutants, the principle of mutation has been accepted by many students of evolution as a working hypothesis; and many are now endeavoring to determine the extent, frequency, and behavior of such mutants.

According to the current view a mutation may be a variation relatively great or small, involving a single unit character or a group of such characters. The mutation is often of greater, but may be of lesser, extent than the fluctuation, and the existence of the two types together may lead to much confusion. Far more careful analytical work will be required before it may be possible fairly to estimate the respective value in evolution of mutation and fluctuation, or indeed properly to distinguish types of variation. There can be no doubt that striking cases are on record of the occurrence of saltation; but it is obvious that the extreme supporters of the mutation principle, by the definition and explanation of the term, actually exclude the possibility of any such phenomenon as transmissible fluctuation.

Tower and Blaringhem working with beetles and with corn respectively have reported some results particularly interesting in this connection. After demonstrating the effect of environment in producing continuous variation in Chrysomelid beetles within the range of the species, Tower reports a striking case of difference in behavior.

The offspring of certain pairs of beetles showing precisely the same variation in spot characters were compared. The offspring of one pair transmitted the variation, while those of other pairs were unable to do so, varying toward the mean of the species. Blaringhem was able through a variety of injuries to produce certain abnormalities of corn flowers, especially the production of grains in the staminate inflorescence. This abnormality was not generally transmissible, yet it was transmitted in a few cases, and even the degree of transmission was found to be variable.

288. Mutation and crop improvement. — The principle of mutation appears to be particularly important in crop improvement. Taken in conjunction with the facts of alternative inheritance, subsequently discussed, it directs attention to uncommon individuals and types, and to the greater probability of securing permanent and immediate improvement by the isolation and breeding of such forms.

No one has contributed more to the method and results of selection work than Nilsson, the Swedish investigator, whose work has been made a special study by De Vries. Nilsson devoted particular attention to the cereals, and his method of selection was founded upon the discovery that " a protean group of types was found to constitute each so-called variety. These types were seen to be different from one another in a previously unsuspected degree, covering a range of variability adequate to comply with almost all the needs of practice." [1]

The practical success of the work of Burbank and others seems to rest upon a careful search for variable forms;

[1] De Vries, "Plant Breeding," p. 68.

the utilization of large numbers, in order that there may be more chance for variation; and in the detection and isolation of the unusual individual or type.

HEREDITY

In the production of plants there are two primary requirements, — there must be (1) the seed or propagative parts, and (2) certain favorable conditions for growth and reproduction. The one is a biological mechanism which has behind it ages of ancestors determining specifically or racially what type of plant there shall be; the other is a complex of physical and chemical factors conditioning what kind of individual there shall be. The embryo plant possesses its particular hereditary possibilities, and it is encompassed by an environment which sustains it or subjects it. Heredity and environment are therefore forces closely linked together in biological investigation. Environment is important in molding heredity, and heredity constantly affects the method of response to environment. All biologists agree that either structural or functional adjustments to environment may ultimately become hereditary; but a chief tenet of Weismannism is that no change is hereditary which does not affect the germ cells.

There is at present great activity in the study of heredity, a manner of cell behavior which we may now tentatively define as being concerned with the transmission through successive generations of racial and individual characters. A fundamental study of transmission is properly termed Genetic Physiology, or simply Genetics.

It finds direct practical application in all the practices of plant and animal breeding.

289. Nonsexual reproduction and heredity. — In nonsexual reproduction a part of an individual reproduces a new individual, and the latter commonly resembles the former as closely as environment or the conditions of its growth will permit. In this case we may scarcely speak of heredity or transmission in the usual sense; yet it is important to recall that whatever the nature of the part used for such vegetative multiplication, it retains the racial or specific characteristics of the plant from which derived. The propagative part or scion usually includes one or more buds. Reduced to the lowest terms conceivable, it might be a single vegetative cell. In at least two cases among flowering plants an epidermal cell may develop a bud, and this bud reproduces the plant. In any case it is remarkable that a single cell, or even a group of meristematic cells, should be able to reproduce so completely all the qualities of a complex adult. Bud variations may occur in plants propagated by nonsexual means, yet most clonal varieties are said to be fairly constant.

290. Sexual reproduction and heredity. — In sexual reproduction, individuals contribute characteristics through the two gametes or uniting cells, and through this union two lines of ancestry are united in one organism. As already noted, in the angiosperms these gametes are a nucleus, with little or no accompanying cytoplasm, from the pollen tube and an egg cell in the ovule; these microscopic, protoplasmic units must carry all the characteristics entering into the organism. This organism will not commonly resemble in absolute detail either parent, nor

will it be an exact mean between the two, as a rule, especially where the parents show contrasting characters. It may show distinctive characteristics of both, perhaps some characteristics evident only in more distant ancestors, and others which may seem to have been modified, or which may appear to be entirely new.

The problems respecting the method of transmission are important, and the theories offered in explanation are both interesting and valuable; but the physiological picture is as yet more or less indefinite. The evidence derived from a minute study of the cell, or cytology, may be of assistance, but it is not to be expected, in general, that any single characteristic of the organism will leave a special morphological imprint upon the nuclear structure.

291. The early studies. — The early studies upon heredity yielded many valuable observations, yet they were disappointing with regard to definite results and to the development of special methods for attacking the general problem. Kölreuter, Knight, Gärtner, and others accumulated interesting data. Galton employed statistical methods, and his studies of pedigree records led him in 1897 to announce his famous "law of ancestral heredity." By this hypothesis, assuming unity as the total hereditary possession of any organism, he assigned diminishing values in a geometrical series (the total approaching unity) to the ancestors in preceding generations, from parents to those more remote, averaging as follows: parents one half, grand-parents one fourth, great-grand-parents one eighth, etc. This conception may be regarded, perhaps, as an expression of the practical results of complex hereditary influences, through many generations; but from it we seem

to get no indication of a particular method in heredity, and no possible analysis of the independent characters concerned. As a matter of fact, in Mendelian inheritance, subsequently discussed, it will be apparent that certain ancestors may contribute nothing, or some few characters only.

292. Types of inheritance. — There are apparently several distinct types of hybrid inheritance, such as blended, intensified, mosaic, heterogenous, and alternative. Three of these may be briefly characterized as follows: —

1. *Blended inheritance.* — The crossing of forms distinct with respect to any character yields offspring possessing this character to a degree intermediate between the parents. Some cases of apparent blends are questioned, and much more study of this type is required.

2. *Intensified inheritance.* — The crossing of forms distinct with respect to any character (*e.g.* size) yields offspring possessing that character more highly developed than either parent. Certain plums produced by Burbank are apparently of this type.

3. *Alternative inheritance.* — The crossing of forms distinct with respect to any character yields offspring which resemble one parent only; but the hybrid nature of this first generation is shown by its offspring. In the latter there is segregation, as explained later, in such manner that each character appears practically unchanged in a part of the offspring.

293. Recent studies. — The newer studies upon heredity practically began with the new century, and with the rediscovery of work done nearly half a century earlier. These investigations are in a large measure concerned

with alternative inheritance in hybrids, that is, with offspring from parentage showing contrasting characters. The work has resulted from a clear appreciation of certain fundamental observations. A single case may serve to typify the simplest form of the problem: Bearded wheat is crossed with beardless. Will the progeny be bearded, beardless, or intermediate? What will happen in succeeding generations? For the development of this line of inquiry, we are indebted first of all to Gregor Johann Mendel, — Priest and later Prälat of the Königskloster of Brünn — and to De Vries, Bateson, Castle, Correns, Tschermak, and many others. Mendel's important contribution was published in 1866, but it attracted no attention and was practically lost to the scientific world until rediscovered in 1900.[1]

294. Mendel's experiments. — Mendel had followed carefully the work of such predecessors in this line of investigation as Kölreuter, Knight, Gärtner, and others. He was particularly interested in what has been characterized as the constant appearance of the same hybrid forms when any two species are crossed. He sought to determine the number of such forms which may arise, the conduct of these in the succeeding generations, and the relations of the forms one to another from a numerical or statistical point of view. He had an unusually clear idea of the indications which should be possessed by the species employed in crossing in order to demonstrate the points in a definite manner. He declared that species to be

[1] For a comprehensive, bibliographical sketch of Mendel, the student should read the notice of him in Bateson's "Mendel's Principles of Heredity," pp. 304–316.

crossed should possess differentiating or contrasting characters; that the hybrid offspring should offer the possibility of being readily protected from foreign pollen; and that the offspring should be, with respect to fertility, unaffected by the inbreeding process necessarily pursued.

He found in the common garden pea (*Pisum sativum*), and other related forms, promising material for his work. After testing for two years the constancy of thirty-four varieties, proceeding with great care, he selected those which showed well-defined contrasting characters, — in all, seven combinations. We may consider three of the typical cases with a single differential character-pair (later termed simple allelomorph, or allelomorphic pair) as follows: —

(1) Difference in color of cotyledons; yellow *vs.* green.

(2) Difference in the color of the seed coats; white *vs.* colored.

(3) Difference in size; tall *vs.* dwarf.

Like Darwin and others who were interested in a more or less similar line at the same time, he recognized the necessity of dealing with large numbers in order that individual errors might be avoided as far as possible. From the crosses obtained with the strains showing the contrasting characters above mentioned, he found that with respect to these characters all of the hybrids resembled one of the parents; that is, there was no blending of these qualities. The character which appeared in the hybrid of the first generation, known as the F_1 generation, was termed the dominant of the pair, and that character which was veiled or latent in the F_1 was termed the recessive. In the three cases above the dominant characters were yellow cotyledons, colored seed coat, and tall habit. No transitional

FIG. 137. Hybridization of Begonias: plants to the extreme right and left, parental types; plant in the center, F_1 generation.

forms were found in the hybrid generation, and in these cases reciprocal crosses gave in the F_1 generation plants entirely alike.

A summary of the results of the F_2 generation is of special interest. Upon planting the seed of the F_1 generation there resulted, in the first case, 258 individuals; and these yielded in the F_2 generation 8023 seeds, of which 6022 were yellow and 2001 green. In other words, the relation of yellow to green was 3.01 : 1. Where color in the seed coats was a contrasting character there were 929 plants in the F_2 generation, of which 705 produced colored seed coats, correlated also with color of blossoms; and 224 produced white seed coats, correlated with white flowers. In this instance the proportion was 3.15 : 1. In the third case, there were in the F_2 generation 1064 plants, of which 787 were tall and 277 dwarf, or a ratio of 2.8 : 1.

In each case one fourth of the individuals, showing the recessive character, breed true in all subsequent generations, that is, in F_3, F_4, etc. In analogous manner one fourth of the whole number of F_2 individuals (one third of the apparent dominants) breed true as dominants. The remainder, one half, are hybrid dominants and break up in the F_3 generation exactly as did the whole number in the F_2 generation. This method pertains through successive generations. It is therefore apparent that the F_2 generation may be represented thus: $D + 2\ D(R) + R$, in which D represents dominants, R recessives, and D(R) hybrid or impure dominants, in which only the dominant character is evident. The latter are here indistinguishable from dominants, except as they show segregation in the next generation.

295. Purity of the gametes. — As a result of these hybridization studies, Mendel naturally developed his theory of the purity of the gametes, founded substantially in this way: In the case of the hybrid between a tall (T) and a dwarf (S) pea, for example, the male gametes in equal number will carry the character tallness or dwarfness, never both; and so also with the egg cells. Assuming large numbers, these gametes, uniting by the law of chance (without selective fertilization), would yield, tallness being dominant, —

Tall with tall or TT (homozygote)
Tall with dwarf or T(S) (heterozygote)
Dwarf with tall or (S)T=T(S) (heterozygote)
Dwarf with dwarf or SS (homozygote)

from which we get T+2 T(S)+S. The essential features of Mendelism are dominance and segregation, and these phenomena are sufficiently important to-day to receive unusual attention. It has been well shown that many Mendelian character pairs may be expressed conveniently in terms of presence and absence of a single character. Either presence or absence may be dominant. The idea of the purity of the gametes requires modification, at least with respect to certain characters.

296. Results of segregation. — In corn yellow kernels are dominant over white. Indicating the yellow by Y, the white by W, and the white in the hybrid, where it is inevident, by (W), the following diagram indicates the method of segregation in five generations, and the relative number of pure dominants, recessives, and hybrid dominants in the hypothetical case where the rate of increase is fourfold: —

Generation	Dominants	Hybrid Dominants	Recessives
Parent	(dominant yellow) Y	×	W (recessive white)
F_1		Y (W)	
		Y (W) + (W) Y	(W) Y
F_2	Y	or 2 Y (W)	W
		2 Y (W) + 2 (W) Y	
F_3	4 Y 2 Y	or 4 Y (W)	2 W 4 W
		4 Y (W) + 4 (W) Y	
F_4	16 Y 8 Y 4 Y	or 8 Y (W)	4 W 8 W 16 W
		8 Y (W) + 8 (W) Y	
F_5	64 Y 32 Y 16 Y 8 Y	or 16 Y (W)	8 W 16 W 32 W 64 W
	120 Y	16 Y (W)	120 W

Upon the principle of the purity of the gametes and the combination of these according to the law of chance, it becomes a simple mathematical problem to determine the number of combinations resulting from a cross in which two or more character pairs are considered.

297. Tomato characters. — To accord with Mendelian results every plant may be regarded as made up of a cer-

FIG. 138. Hybridization of tomatoes: parental types (top row), Honor Bright and Yellow Pear; F_1 generation (2d row) quite uniform; F_2 generation (3d and 4th rows) showing segregation. [Photograph by H. L. Price.]

tain number of unit characters, which may be contrasted in different forms or varieties. Price and Drinkard have determined thirteen such alternative character pairs

for the tomato. These may serve as a further example of unit characters, and they are listed below, the dominant unit of each pair being placed in the middle column: —

Fruit Shape:	Spherical or Round .	Pyriform
	Two-celled	Many-celled
	Roundish-conic . .	Roundish-compressed
Fruit Color:	Red Fruit	Pink Fruit
	Red Fruit	Yellow Fruit
	Pink Fruit	Yellow Fruit
	Yellow Fruit Skin . .	Transparent Fruit Skin
Fruit Surface:	Smooth	Pubescent
Foliage:	Normal or Cut Leaf .	Potato Leaf
	Pimpinellifolium Leaf	Normal Leaf
	Green Leaf	Yellow Leaf
	Normal or Smooth Leaf Surface . . .	Rugous Leaf
Stature:	Standard Stature . .	Dwarf Stature

298. Chromosome relations. — A material basis for certain types of inheritance, especially Mendelian phenomena, seems to be found in the behavior of the chromosomes. The reduction division, occurring in seed plants in the formation of the microspores (ultimately pollen) and megaspores (ultimately embryo-sac) is the important stage. In this the $2x$ (somatic or diploid number of chromosomes is reduced to the x (gametic or haploid) number. It is generally held that the essential features of this division are two: (1) close association in pairs (bivalent chromosomes) of paternal and maternal chromo-

somes, in which association, particularly, mutual character influences may find explanation; and (2) separation of the previously associated chromosomes (members of a pair), one to each of two daughter nuclei, thus segregating

Fig. 139. Hybridization of tomatoes: same fruits as shown in preceding figure, in section. [Photograph by H. L. Price.]

maternal and paternal characters. A comprehensive discussion of cytological relations is entirely beyond the scope of this work.

299. Selection. — Selection of forms for hybridization

requires intelligent care. Hybridization is primarily useful in order to effect the combination of desirable characters and the elimination of undesirable ones. Nevertheless, it is generally agreed that in some cases of alternative inheritance there may be left an influence of the cross, so that the characters may not reappear in their original purity. Moreover, as a result of hybridization latent or reversionary characters may appear, and crossing has a tendency to intensify variability.

A knowledge of Mendelian behavior has necessitated a change in the methods of selecting hybrid offspring. In alternative inheritance there can be no selection in the F_1 generation. In the F_2 generation selection for the pure recessives may be made. However, since homozygous dominants usually distinguish themselves from heterozygous dominants only in the absence of segregation in subsequent generations, it is necessary to isolate individuals and to test these in breeding plots. When several character pairs are involved, all of which require consideration, selection with respect to dominant characters may become very complex and tedious.

LABORATORY WORK

Variation. — Utilizing convenient plants in the greenhouse or in the field make a careful study of variation with respect to single characters readily enumerated, or measured. The number of ray flowers, or of bracts in certain composites, the number of flowers in a cluster, the number of eyes upon potatoes, the number of leaflets in compound leaves, the difference in weight of grains or corn, and many other similar characters may be employed. In such cases the counts or measurements should be made within the single variety. Determine the classes of

variation, construct curves and prepare a report which shall include the results of the study made, together with an abstract of one or more of such papers as the following: —

DAVENPORT, C. B. Statistical Methods. Pp. 19–41.
DAVENPORT, E. Principles of Breeding. Pp. 681–703.
HARRIS, J. A. Amer. Nat. **43**: pp. 350–355; *ibid.*, **44**: pp. 19–30.
LUDWIG, F. Biometrika. **1**: pp. 11–29.
PEARSON, K. Grammar of Science. Pp. 381–402.
SHULL, G. H. Amer. Nat. **36**: pp. 111–152.

Compare, if possible, the curves of variation with respect to any character in two populations grown under dissimilar conditions.

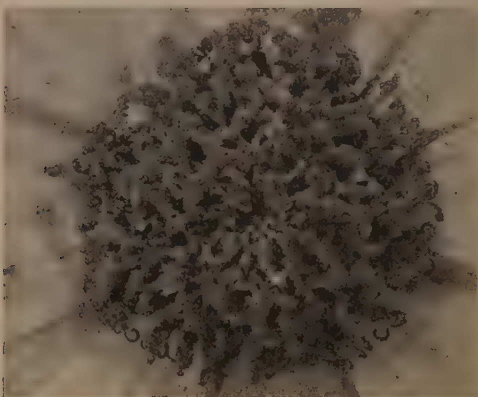

FIG. 140. Dahlia flowers with bursting anthers. [Photograph from Bureau Plant Industry.]

Heredity. — Laboratory work upon heredity covering only one or two periods may be only suggestive, or may give opportunity for the presentation of materials which may be subsequently worked up as a report. Practical studies are preferably confined to the following: —

1. A study of the methods and manipulation of crossing, consulting such references as —

BAILEY, L. H. Plant Breeding. Pp. 344–358.
OLIVER. Bureau of Plant Industry. Bul. **167** : 39 pp.

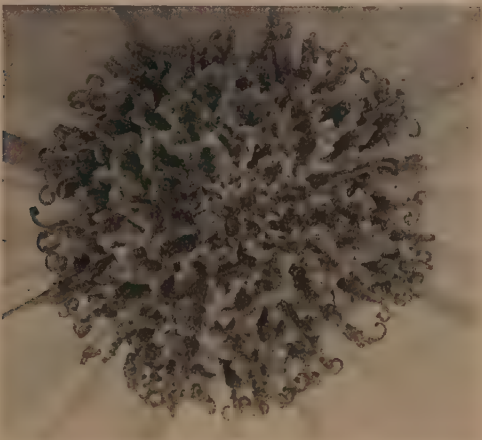

FIG. 141. Dahlia flowers after depollination by means of a stream of water. [Photograph from Bureau Plant Industry.]

2. The results of crossing. In the latter case parents, together with first and second generation crosses, should be compared with respect to characters, following the suggestions in sections 294–297. Fresh material is most desirable, but if it may not be had at the time desired, alcoholic or dried material will serve adequately for the study of many characters.

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CHAPTER XX

GROWTH MOVEMENTS

All plants possess the power of movement to at least a limited extent. The various types of movement and their relations constitute a considerable part of plant physiology as commonly presented. Here, however, it will be possible merely to outline portions of the subject, which may be further pursued in the special literature. It is entirely beyond the present purpose to consider locomotory movements, likewise the phenomenon of dehiscence, and other effects due to swelling and contraction. Nevertheless, special movements of turgor are included on account of their closer relationship.

Movement may occur within the protoplast, and may be limited to the cell, or it may occur in such manner that complex structures exhibit change of position or change in the direction of growth. As popularly regarded, those plants possessing roots are fixed in the soil or other substratum, and movement is only associated with such striking changes as may be seen in the sensitive plant (*Mimosa pudica*), the Venus's-flytrap (*Dionaea muscipula*), or certain climbers and twiners. As a matter of fact, movement is almost inseparable from growth.

The elongation of root or shoot is a type of growth movement. There is, furthermore, a remarkable variety

of growth responses resulting in curvature or orientation of members. As previously indicated, the movements of plant members are now regarded as primarily of two types, spontaneous (autonomic) and induced (paratonic). The former are little understood. It is not always possible to distinguish positively between the two types, or the movement may be the result of conjoint (internal and external) stimuli. In general, growth movement is a fundamental requirement in the effective adjustment of organisms to their environment. A study of the phenomena is more important educationally in liberalizing our views of plant relations than of any direct assistance in special problems of plant production.

300. Stimulus and response. — The relations of organisms to growth factors have been considered, but it is necessary to refer again to the environmental forces which condition plant activity. When the environment is favorable the plant is regarded as exhibiting the condition of tone; and the effect of each factor or of the various factors severally is a tonic influence. The factors concerned are those essential in growth, especially oxygen, moisture, food-supply, light, and heat. They are sometimes known as the formal growth conditions. Some of these, and likewise other environmental factors, may act not as tonic influences but as special stimuli releasing growth responses, that is, movements.

The plant is not merely a complex mechanism; it is, when in a condition of tone, a source of readily releasable energy, — growth energy. It requires a stimulus to make this energy manifest, but it appears unnecessary that the stimulus should impart force. As so often pointed out,

the stimulus required is analogous to the pressure of the finger on the electric button which sets at work powerful dynamos. The pressure upon the button has no relation to the amount of work which will be accomplished by the machines thus released. When a stimulus affecting the plant is external, its relations to response may be worked out with a fair degree of success; but the methods of action of internal stimuli are almost entirely unknown. In the action of any stimulus upon a sensitive organ there are to be distinguished primarily (1) perception, (2) transmission, and (3) reaction or growth response. Commonly the perceptive region is at no great distance from the motor or responsive part; yet in certain cases the stimulus may be transmitted through considerable intervening tissue. Practically nothing is known regarding the mechanism of transmission. Perception often resides in the terminal portion of the organ, but not always in the formative region.

In order to produce response a stimulus must act usually for a certain interval of time, and this interval (presentation time) depends upon temperature and other growth conditions. The visible response to the stimulus may be prompt, as in the case of many tendrils, or it may be delayed for several hours. The interval between stimulation and response (reaction time) is usually longer than that of presentation.

301. Tropic curvatures. — Every plant exhibits a normal form and habit, and its members are arranged in a definite manner with respect to one another and to environmental forces. Tropic curvatures are commonly the results of irritable growth responses manifest when the

normal position of a sensitive structure is shifted, or when this member comes under the influence of new or intensified forces, or of forces acting from a new direction. The curvature of horizontally placed roots toward the earth and the bending of the hypocotyl of a seedling exposed to one-sided illumination are familiar illustrations.

The importance of a means of orientation in order to assume or restore the normal is obvious. If the reaction of the growing organ results in orientation parallel to the direction of the exciting force, the organ is parallelotropic, while one assuming a position at an angle to the direction of the stimulus is plagiotropic, — diatropic being at right angles to the path of the stimulus. The tropic movements here discussed are effected in growing structures, or those in which growth may be initiated, and they cease with incapacity for growth. Moreover, the stimulus remaining the same, the rapidity of growth determines the promptness of the response, or reaction time.

Attention has been directed to the tropic responses of plants to light (phototropism) and to heat (thermotropism). Other stimuli inducing reactions are such as gravity (geotropism), contact (thigmotropism), moisture (hydrotropism), electricity (electrotropism), and certain chemical agents (chemotropism).

302. Geotropism. — The vertical position of the main axis of most plants is as apparent as the erect posture of man. A seed may be planted in any position in the soil; but as soon as sufficient growth is made the parallelotropic position of the axis is assumed, with the root directed straight downwards (positively geotropic) and the stem directly upwards (negatively geotropic). Germinating

seed in a moist chamber pinned in a horizontal position will respond to the stimulus of gravity by growth curvatures in the same manner. Secondary roots and branches take up plagiotropic positions, but in the remote branches of the root little geotropic response is manifest. Shoots from a fallen trunk assume the vertical position. If the terminal shoot of spruce is cut off, one or more lateral shoots of the first whorl may be raised into the vertical position. The erection of the jointed stems of grasses is effected by curvatures in the nodes, and these stems are particularly interesting for study.

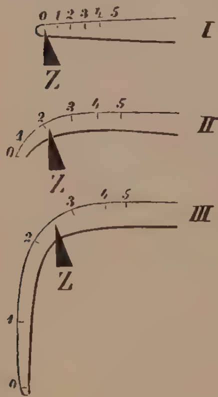

FIG. 142. Geotropic curvature of root of *Vicia Faba*; horizontal position (I), after 7 hrs. (II), and after 23 hrs. (III). [After Sachs and Noll.]

Geotropic response is not a question of weight, and this is shown by the diverse reactions of the main axis and branches. Furthermore, there is no geotropic response when gravity is eliminated, as by revolving seedlings in a vertical plane on a klinostat geared to make one revolution in about fifteen minutes. On a klinostat rotated horizontally at a low rate of speed the usual stimulus of gravity is felt; but when rotated at a higher rate of speed the root grows outward and toward the horizontal, and the shoot inward and toward the horizontal, depending upon the rate of rotation.

In the case of the root the perceptive region is usually confined to about one millimeter, or less, at the very tip,

while curvature occurs in the region of greatest growth. The time required for perception (presentation time) varies from a few minutes to several hours. Reaction time is often several hours, and response is evident even if meanwhile the position of the organ is again shifted. The mechanism of geotropic perception is not clearly understood. An early mechanical theory of Knight has found new life in the statolith theory of Němec, Haberlandt, and others. By this hypothesis it is assumed that in shifted structures the sinking of certain cell products, especially starch, to the bottom of the cell produces a change of pressure, and it is this change which furnishes the excitation.

303. Thigmotropism. — The capacity for thigmotropic response, or growth curvature induced by contact, is most highly developed in tendrils.

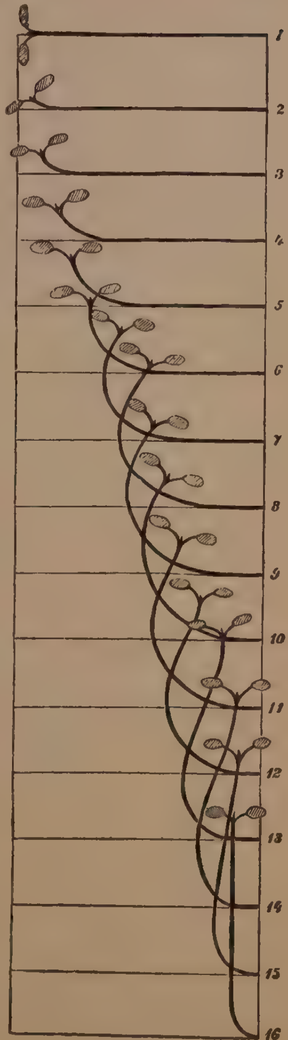

FIG. 143. Diagrammatic view of geotropic curvature in an etiolated hypocotyl, horizontally placed. [After Noll.]

Roots and leafy shoots appear to possess this power to a very limited extent.

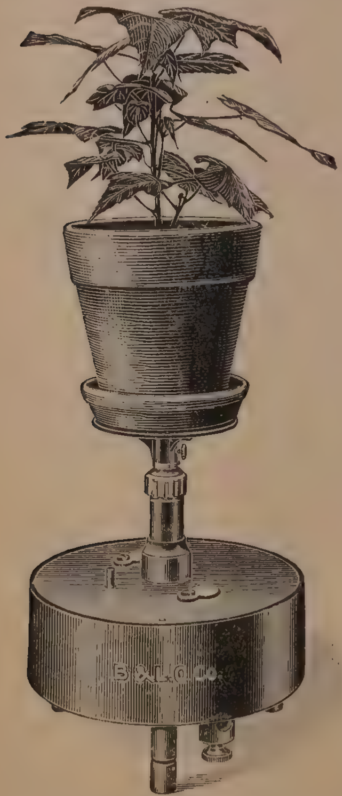

Fig. 144. Demonstration klinostat, after Ganong, vertical arrangement. [Illustration from Bausch and Lomb Optical Co.]

Plants producing tendrils are particularly well equipped to climb aloft, supporting themselves by the attachment of these to any small supports, especially to those horizontally placed. By this means such plants as the grape vine, wild cucumber, Passiflora, and many others are enabled to climb through trees and layered vegetation, whereas twining plants commonly require a support which is more or less vertical.

The tendrils are commonly axillary or supernumerary branches devoid of leaves, or leaf-parts entirely lacking blades. Sometimes, however, petioles of normal leaves or extended leaf tips may function as tendrils. These structures commonly exhibit dorsiventrality, and a right and

left flank may be differentiated. They usually complete their growth within a few days, so that the plant may be attached to its supports almost as rapidly as the shoot elongates.

The terminal part of the tendril is the more perceptive region, and commonly the under surface exhibits greater sensitiveness. Both surfaces and flanks may, however, respond to contact stimuli. When the tendril is from one-fourth to one-third grown, it exhibits marked autonomic nutations, and the swinging of the tip through space brings it into contact with any objects in the range of this motion or of swaying movements caused by wind. Scraping the surface of the tendril against a suitable support (especially repeated scraping) is followed by coiling and close attachment around the object. The tendril is now fixed at both ends, the prompt grasping of the support being in part, apparently, due to turgor movements. After attachment growth proceeds more rapidly on the upper surface, and the tensions resulting throw the tendril into a close coil, once or more reversed.

Fixation by means of tendrils affords not merely secure support, but the attachment at many points affords a general elasticity and freedom from severe shock well known through the principle of vehicle and car springs.

304. Chemotropism. — The curvature and growth of roots, pollen-tubes, or fungous hyphæ in response to the stimulus of chemical agents is chemotropism. At one time it seemed that chemotropic response, especially positive chemotropism, might commonly determine the direction of growth in roots, penetration of parasitic fungi, and other phenomena. Further study has developed the

probability that positive chemotropism is not a highly developed response. It may occur in roots and pollen-tubes, although the evidence is not entirely convincing; while serious doubt has been thrown upon the existence of positive chemotropism in fungous hyphæ.

305. Nutation. — The tips of growing axes or other plant members are not as a rule extended in a straight line. Instead, they nod here and there or commonly trace an irregular spiral, the projection of which yields a series of more or less circular or elliptical figures. This type of movement is called nutation (circumnutation). It was extensively studied by Darwin, and the main effects together with some of the important relations were clearly set forth at that time.

The type of curve varies with the growth relations. In stems which are radially symmetrical nutation results from unequal growth in the vertical segments. The effects produced are accounted for by greater growth in each segment successively around the stem. When asymmetry occurs, and especially in flattened or dorsiventral organs there is more likelihood that the movement will tend toward narrow ellipses or even the back-and-forth linear type. The extent of the movement depends upon the unevenness and rapidity of growth. It is generally greatest in organs growing rapidly, such as tendrils and climbing shoots, and the whole of the growing region may be involved. Nevertheless, the pronounced nutation of twiners does not begin, as a rule, until after a few internodes are produced. Tendrils, likewise, show little nutation during the early stages of growth, and the movement ceases in matured organs.

"All stages are shown between trifling and pronounced nutation, according to the plant, to the stage of development, and to the external conditions. The curves are not always regular and similar, even when there is a pronounced tendency to linear, elliptical, or circular nodding, as the case may be. Even when the last named is most pronounced it may temporarily alter into to-and-fro pendulum movements."[1]

The stimulus to nutation is in most cases primarily internal and spontaneous, but it may be conditioned, initiated, or in large part induced by other agencies, especially by gravity and light. The time required for the completion of a single ellipse, or back and forward movement, may be one or two hours or as many days; and when there is a tendency toward the latter type of nutation, the movement of the organ is least rapid near the point of reversal.

306. Nastic curvatures. — In most of the types of growth response already considered the stimulus is unilateral and the curvature may occur in any plane. Fairly well distinguished from the preceding are those cases in which the structure of the organ is such that response is usually limited to orientation in a single plane, whether the stimulus is diffuse or unilateral. Bilateral or dorsiventral members, such as leaves, floral leaves, and flattened stems, are structures of the type above noted. The bendings resulting in such organs are known as nastic curvatures, and they may be distinguished by the same prefixes as in the other cases to denote the type of stimulus, thus photonasty, thermonasty.

[1] Pfeffer (Ewart), *Physiology*, **3**: p. 20.

Nastic curvatures, however, are not necessarily the result of external stimuli, hence they may be either autonomic or paratonic.

In the development of leaves (section 181) there is usually a growth response whereby the under or dorsal surface grows faster, yielding an upward curvature (hyponasty). As a result of this each leaf in turn becomes a part of the bud. Later the growth on the upper or ventral surface is more rapid and there is outward bending (epinasty) during exfoliation. There may be a recurrence of epinastic and hyponastic curvature under the influence of various stimuli until maturity of the leaf. Growth upon the upper surface called forth by light is a paratonic nastic bending, or photepinasty.

307. Nyctitropism. — The old idea of floral clocks was founded on the observation that flowers of diverse species open and close with different light and temperature relations. There are some flowers which remain closed during the night, opening in the early morning with increased temperature or sunshine. Others are less readily stimulated and remain closed until the conditions are further intensified. Again, some blossom when the heat of the day begins to decline, while the night-blooming Cereus and certain other flowers bloom at night.

Movements of floral leaves have been shown to be typically nastic growth movements and they disappear as soon as the power of growth is lost in these organs, unless accompanied by special basal articulations which may show turgor movements.

Quite as characteristic are the sleep movements of leaves in a number of families, especially Leguminosæ and Mi-

mosæ. All plants possessing jointed leaves do not exhibit the same behavior. Nyctitropic movements are commonly due to changes of turgidity, and growth is not usually involved. The articulations are cushions in which cortical tissue predominates. Under stimulation the dorsal and ventral halves give osmotic changes unequal in rapidity so that movement is brought about.

LABORATORY WORK

Geotropism. — For a few observations upon the geotropism of roots fairly large seeds are desirable, such as those of peas or beans. Germinate the seed in moss or on paraffined wire netting over water. When germination has progressed to the extent of a few centimeters, the roots may be marked off with India ink as for determining the region of extension. The growth curvatures are then to be followed by placing the radicles in a horizontal, or any other desired, position. If only a few seed are used, they may be pinned to the lower side of large corks covering jars or dishes partially filled with water.

For a larger number of seed and particularly for observations respecting the effects on side roots, the seedlings may be arranged at various angles on two thicknesses of moistened carpet or felt paper between plates of glass. The plates are clamped together with wooden clothespins, and wads of filter-paper here and there prevent crushing. Place the plates on edge in a moist greenhouse or cover with wet cloths. Observe from time to time, note the results, and shift the position of the plates through ninety degrees after secondary roots are produced. Discuss the results.

Negative geotropism of young shoots may be followed by observing the behavior of bean or pea seedlings when the pots are placed horizontally. Determine also the time of presentation and of reaction for such seedlings grown in very small (2 inches) pots. Compare the presentation time at 12 to 15° with the interval at 25 to 30° C.

Secure shoots of Tradescantia or of oats embracing several

nodes; pin the basal node to a cork or block of wood and follow the process of erection.

With the special instructions given determine the behavior of roots and shoots of seedlings when gravity is equalized through vertical rotation upon the klinostat.

Chemotropism. — The existence of positive and negative chemotropism would seem to be established and some of the chemotropic relations of pollen-tubes may be conveniently and easily observed. Utilize pollen known to germinate freely, such as that of *Tradescantia virginica* and *Narcissus Tazetta* and prepare hanging-drop cultures as for pollen germination. When the grains begin to germinate, introduce into the drops bits of the stigma of the plant from which the pollen was taken. Ascertain if these stigma bits or if particles of any vegetable proteins (albumins and globulins) exert any influence on the direction of growth of the tubes.

If time for more extensive study is available, consult the paper by Lidforss (or follow special instructions), employ Pfeffer's capillary tube method, and install the necessary experiments.

Growth and movement of tendrils. – Utilizing any tendril-bearing plant available in the greenhouse or field, select several tendrils about one fourth grown, mark off into ten or twenty spaces by means of India ink, and determine the region and period of growth, also the daily percentage increase in the different longitudinal segments.

Review in suitable literature the more extensive accounts of tendril movements, and make an extended observation upon the behavior of one type, presenting the results in the form of a report.

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TEXTS. *Barnes, Detmer, Ganong, Jost, MacDougal, Pfeffer.*

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